18 APR 1995		(1940)	
14 MAY 1996		(3459)	

OXFORD MEDICAL PUBLICATIONS

BORRADAILE'S MANUAL OF ELEMENTARY ZOOLOGY

BORRADAILE'S MANUAL OF ELEMENTARY ZOOLOGY

Revised by

W. B. YAPP, M.A.

Lecturer in Zoology, University of Birmingham

FOURTEENTH EDITION

LONDON

OXFORD UNIVERSITY PRESS

NEW YORK TORONTO

1963

Oxford University Press, Amen House, London E.C.4
GLASGOW NEW YORK TORONTO MELBOURNE WELLINGTON
BOMBAY CALCUTTA MADRAS KARACHI LAHORE DACCA
CAPE TOWN SALISBURY NAIROBI IBADAN ACCRA
KUALA LUMPUR HONG KONG

First Edition 1912
Fourteenth Edition 1963

PRINTED IN GREAT BRITAIN

CONTENTS

		PAGE
1.	Introductory: The Animal Organism	1
2.	Amœba	24
3.	Flagellate Protozoa	34
4.	Monocystis	41
5.	Ciliate Protozoa	45
6.	The Protozoa as Parasites of Man	61
7.	The Classification of Protozoa	76
8.	Sponges	81
9.	Hydra and the Cœlenterates	86
10.	Flatworms	115
11.	Roundworms	131
12.	Parasitism	144
13.	Earthworms and other Annelids	155
14.	The Cœlomate Body	186
15.	The Crayfish	194
16.	Cockroaches	218
17.	Arthropods and Insects	232
18.	Molluscs	264
19.	The Starfish	286
20.	The Lancelet	298
21.	The Dogfish	310
22.	The Frog	344
23.	The Pigeon	389

		PAGE
24.	THE RABBIT	414
25.	MAMMALS	474
26.	THE CELL AND MAMMALIAN HISTOLOGY	498
27.	THE CLASSIFICATION AND STRUCTURE OF VERTEBRATES	548
28.	EMBRYOLOGY	632
29.	HEREDITY AND CELL DIVISION	688
30.	THE ORIGIN OF SPECIES	715
	INDEX	737

PREFACE TO THE FOURTEENTH EDITION

THE chief change in this edition is a new chapter on embryology, for help with which I am much indebted to my colleague Dr. J. Cohen. Embryology is a notoriously difficult subject to teach to the beginner, and we have endeavoured to write a chapter which, while it will provide the student with all the information that he is likely to need for examination syllabuses, will give him also a picture of what embryology is about. Corrections and additions to bring the matter up-to-date have been made throughout the book ; for those in the chapters on Protozoa I am grateful for many suggestions from Dr. R. J. S. Hawes, of the University of Exeter. I have also strengthened the physiological side by additions at appropriate points, and in order to keep the bulk of the book down have made some excisions of matter which I believe to be little used. There are some new figures.

I thank all those who have made suggestions for the improvement of the book ; some that I have not been able to use in this edition have been noted for the future.

W. B. Y.

CHURCH END,
January 1962.

PREFACE TO THE THIRTEENTH EDITION

THE twelfth edition of Borradaile, the first major revision since the book was published forty-five years ago, has on the whole been well received both by reviewers and by readers. Complaint was commonly made of the illustrations, both old and new, and with some justification. The necessity for a new edition less than two years after the edition was published has allowed the replacement of some forty-three of these, and I hope that in future editions more will be treated in the same way. I am grateful to all those who have pointed out misprints or *lapsus calami*, all of which have been corrected. I thank also those who have reported errors; if a reviewer finds that any of these remain uncorrected it is because, after consulting the best authorities available to me (including, in two instances, the animal itself) I have come to the conclusion that what I originally wrote was nearer to the truth. I have also tried to remove a few ambiguities, and statements throughout the book have been corrected to accord with new knowledge.

The interest that the book has aroused is very pleasing, but there is one respect in which I cannot agree with some of my critics, who would have liked to see the old morphological basis entirely abandoned. While I agree completely with them on the importance of physiology and ecology, I believe that there is still good reason for not trying to force on students a fusion of the morphological, physiological and ecological aspects of the subject, which, at the level for which this book is written, few of them will understand. I have retained the type-system not, as one reviewer said, because I have never known any other, but because I have seen, as a teacher, as an examiner, and as an attender at scientific meetings, the bad results of attempts to be 'synthetic' or 'comparative' before the student knows the basic facts of morphology. They simply do not work. The sections in this book on parasitism (now put as a separate chapter) and on the cœlomate body, and those on vertebrates at the end, read after those on the relevant types, will give the student of sixteen to nineteen or so, enough on which to exercise his mind (I hope he will do so critically). I intended originally to include a general

chapter on physiology, and may still do so in a later edition. But, with some experience of reducing the whole range of physiology to small compass, I am not sure that such extreme compression can usefully be done.

W. B. Y.

STOURBRIDGE,
August 1957.

1

INTRODUCTORY: THE ANIMAL ORGANISM

BIOLOGY

ZOOLOGY, the science of animals, is a branch of biology, the science of living beings. Of such beings there are various kinds besides the animals ; but all the kinds have important features in common. Rightly to understand any animal is therefore to comprehend properties which it shares with non-animal living beings as well as its purely animal characters. Thus at the outset of our study of zoology it is desirable that we should spend a little time in considering the nature in general of living beings.

LIVING AND LIFELESS

Out of the multitude of material objects that surround us, we distinguish some, as alive, from the rest, which are lifeless —that is, either are dead or have never been alive. It would be helpful if we could set down in precise terms the properties on which we base this distinction.

The commonsense view is that a living being, such as a cow or a tree, grows and reproduces, while a non-living thing, such as a stone or a piece of wood, does not, but a little reflection will show that no precise distinction can be made in these terms. A cow may be capable of reproduction, but for a variety of reasons, such as absence of a bull or infection by a parasite, may not in fact produce offspring ; an ox can never reproduce, but is nevertheless alive, and if it be objected that an ox is in an artificial state through the interference of man, there is the parallel example of the worker bee, which is sterile by nature. It is a matter of common observation that growth, in the ordinary sense of the word, ceases in man relatively early in life, and in old age it becomes negative, if the expression may be permitted. In some of the lower animals, too, ' degrowth ' is known ; thus, if a pond flatworm is starved it decreases in size and appears to reverse its normal trend.

No better definition of life can be made from any of the other properties which have from time to time been proposed for the

purpose. Neither irritability, nor self-preservation, nor respiration is at all times characteristic of things which are called living, and one or more of these properties (as well as growth and reproduction) may at times be found in things which are called non-living. In the limit, it remains a matter of opinion whether the viruses (small particles which cause a number of diseases such as smallpox and measles) should be considered as living or non-living.

In spite of the impossibility of making a definition, there are certain properties which are generally found in things which men tacitly agree to call living, and which are seldom found in things which they do not so call. We will now briefly consider the more important of such properties.

GROWTH

Growth means the increase in quantity of material in a body, and is usually measured, for biological purposes, as increase in dry weight (this word being used incorrectly for mass), that is, weight after free water has been driven off at 105° C. It thus excludes mere addition of water, which may be so rapid and temporary as to be meaningless, and differs fundamentally from increase in size, which may occur by absorption of water or even air. It depends on an uptake of matter from the surroundings, and on this more is said below.

REPRODUCTION

An animal or plant may, by itself or in co-operation with another, produce a new living thing, a process known as reproduction. In a sense reproduction is a consequence of growth, for growth without reproduction would lead to an impossible expansion in size ; this connection is seen at its clearest in an animal like *Amœba* which simply divides into two when it reaches a certain size, but in the higher animals the connection is obscured. The division of a cell of a higher organism (p. 700) though it may take place by a similar mechanism, is philosophically distinct from the reproduction of *Amœba*.

Reproduction always includes, though it may be much more than, the fission or division of an existing body. Whatever may have been its origin, all the evidence suggests that under the

conditions which now exist life never starts anew, but is always passed on from one living being to another which arises from it. A living being which divides to produce others is a parent; those which it forms are offspring. These are always at first unlike the parent. There are certain creatures, like *Amœba*, mentioned above, in which the only evident difference between the offspring and the individual by whose division they arose is the necessary

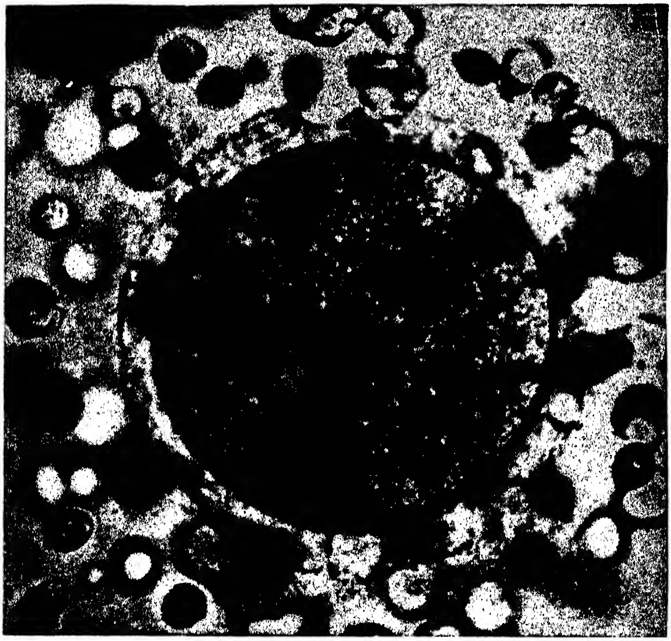


FIG. 1.1.—Human ovum from the uterus. × 480.—From Hamilton, Boyd, and Mossman, *Human Embryology*, 1945. Heffer and Sons, Cambridge.

one of size, but in the great majority of cases there is also an obvious difference in form, the offspring being at first very unlike the parent in structure. This difference is obscured in the case of man and some other animals, where the offspring (Fig. 1.1) undergoes changes in the womb before birth, but it is seen unmistakably in animals which are born in the condition of an egg. In their immature condition the offspring are known as reproductive bodies.

In spite of this unlikeness at starting, the offspring become in time like the parent or parents from which they arose, though

they never resemble them in every detail. The succession of changes which brings this about is called development, and is sometimes straightforward, or direct, sometimes, as in the well-known case of the butterfly, very roundabout, or indirect. In reproduction by budding (Chap. 9) development may take place partly or mainly before fission. Thus the life of an animal or plant is a cycle, in which it passes through a series of stages, beginning with the small and simple reproductive body, and ending with the larger and usually more complex adult, ready to undergo fission again. Every typical individual goes through the same cycle of changes as its parent, resembling in each stage a similar stage passed through by the latter, till it reaches the likeness of the individual that produced it, that is, it shows the property known as heredity. Thus, in the strict sense of the word, reproduction includes the whole life cycle and consists of two distinct processes—fission, and the development of the reproductive body into the adult—for until this cycle has been completed the parent is not reproduced. From this point of view, growth is that part of the process of development by which the reproductive body reaches the size of the adult. At the same time, usually, and perhaps always, the growing individual is undergoing the changes in structure to which we have alluded.

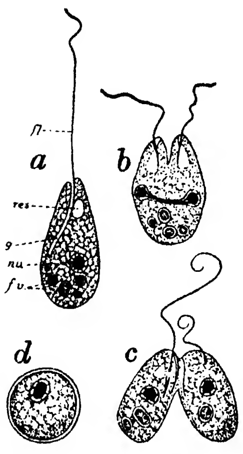


FIG. 1.2.—*Copromonas*, a minute inhabitant of dung. — After Dobell.

a, Adult individual ; *b*, the same in fission ; *c*, two adult individuals in syngamy; *d*, the zygote, enclosed in a cyst.
f.v., Food vacuole; *fl.*, flagellum; *g.*, gullet; *nu.*, nucleus; *res.*, reservoir of contractile vacuole.

SYNGAMY

Here must be mentioned a process which is an essential part of reproduction in many organisms and in all the higher animals. In such organisms the reproductive bodies are of two sorts, each produced only by one of the sexes, and neither sort can develop except after fusion with one of the other sort. That fusion is an example of the process known as a syngamy, union of two distinct living bodies, which occurs from time to time in nearly all species of animals and plants. The bodies which unite are known as gametes, and that which results from their fusion as a zygote. In some of the smallest living beings (Fig. 1.2) syngamy

is the union of fully-grown adults, but in other such creatures (Fig. 1.7), and in all large and complex animals and plants, syngamy takes place only between the reproductive bodies, which are generally unable to develop without it, so that it becomes a necessary part of the reproductive process. In these creatures the reproductive bodies are of a kind known as germ cells, distinguished from other reproductive bodies (free buds, etc.) by their small size and the simplicity of their structure. The germ cells of such creatures are usually of two sizes which unite larger with smaller (Fig. 1.7*C*). In all large and complex animals

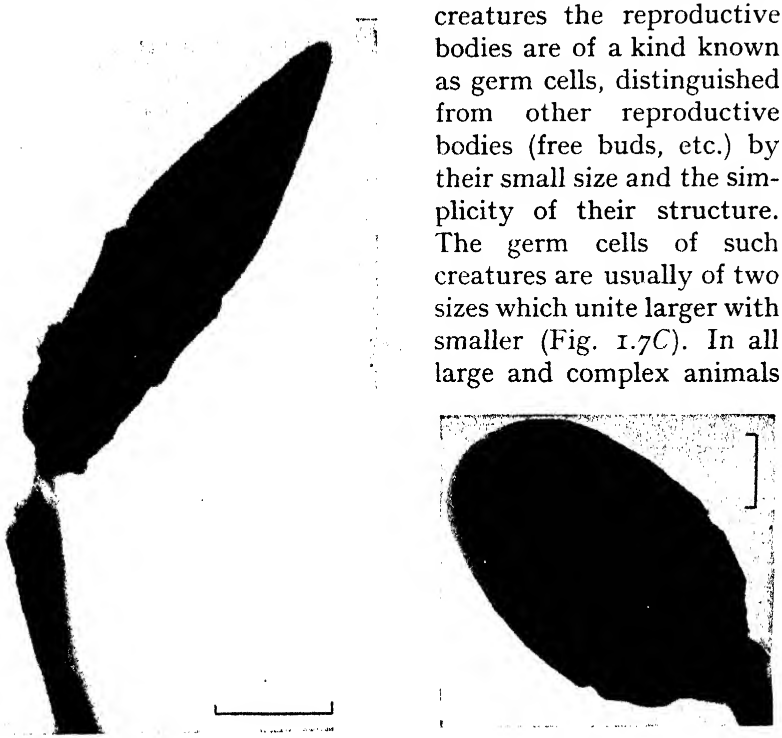


Fig. 1.3.—Heads of human spermatozoa, in side and face view. Electron photomicrographs. The scale is one micron.—From Friedlander, *Proc. roy. Soc. B*, 1952, 140.

(and in some of the smallest) the gametes differ in form and behaviour as well as in size (Figs. 1.1 and 1.3). One is larger and passive, and is called the female gamete, or, in large animals, the egg or ovum. The other is smaller and active, and known as the male gamete or spermatozoon or sperm ; it has usually a tail (flagellum) with which it swims in the fluid in which it is borne, and thus it moves to the egg and enters the latter (Fig. 1.4). This process is known as the fertilisation of the ovum. After it the fertilised ovum proceeds to develop. Ova and spermatozoa are usually formed by different adults, known respectively as female

and male, but in some animals both kinds are formed by one individual, which is then known as a hermaphrodite. If sperms are formed before ova, a hermaphrodite is said to be protandrous; if the ova are formed first, it is protogynous. In some aquatic animals the gametes are set free, and syngamy takes place outside the body of the parent. In others, however, and in all land animals, the ova are kept within the body of the mother, and the male gametes are transferred in the seminal fluid by the male to the body of the female and there fertilise the ova. This transference is known as coition or copulation. Reproduction in which syngamy is necessary before the reproductive bodies can develop is known as sexual reproduction; that in which the reproductive bodies are not gametes is asexual.

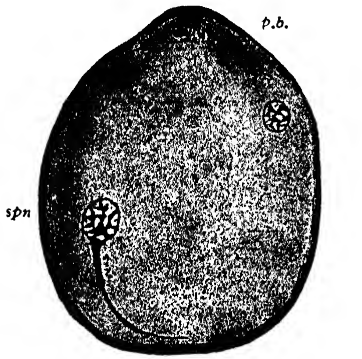


FIG. 1.4.—The ovum of a bat, after the entry of the spermatozoon.—From F. H. A. Marshall, after van der Stricht.

o.n., nucleus of the ovum; *p.b.*, 'polar bodies' (see p. 702); *spn.*, spermatozoon.

In some animals there is a kind of reproduction (parthenogenesis) in which a female germ cell (ovum) develops without syngamy. This kind is best regarded as an aberrant form of sexual reproduction.

The terminology of these processes is in some confusion. Syngamy is the fusion of two cells (p. 498), nucleus with nucleus and cytoplasm with cytoplasm, though one of the two may have little cytoplasm and possibly sometimes has none. The union of nuclei—which is far more important than that of the cytoplasms—is karyogamy; the union of cytoplasm is plasmogamy. The term conjugation has been used as a synonym for syngamy but is best restricted to the peculiar procedure by which syngamy is accomplished in the Ciliata (Chap. 5).

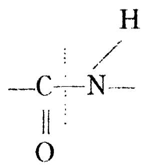
ACTIVITY

Most familiar animals, and some plants, may be said to be active in a way in which a stone is not, although machines have a certain type of activity which simulates that of living things. The activity may be the result of the receipt of a stimulus, that is a change in the external environment, or it may occur without

apparent cause. The first, examples of which are the shaking of the head of a dog when the hairs in its ear are touched and the folding and falling of the leaf of a sensitive plant when it is knocked, has been called irritability, and the second, which may be illustrated by the beating of the heart, automatism. In many cases a distinction is difficult. Irritability differs from mere mechanical change produced by external circumstances, such as the melting of ice, in that the magnitude of the response, as measured by the energy involved, bears no relation to the magnitude of the stimulus. It follows from this, and from the first law of thermodynamics, that the energy for the response must come from within the organism.

ABSORPTION AND ASSIMILATION

Growth requires the intake of new material, and response needs energy, which depends on the breakdown or conversion of chemical substances. The incorporation of food is therefore characteristic of living matter. Two distinct processes may be recognised in incorporation—absorption and assimilation. Before it can be absorbed the food of animals has generally to undergo a preliminary process of digestion, whereby solid or indiffusible nutriment which it contains is made soluble and diffusible. The food must always contain the following materials: (1) water, which is of the highest importance both as an essential constituent of the living matter (protoplasm) and also because it is used in the body for transporting substances in solution, as in the blood and urine, (2) certain inorganic ions, such as chloride and phosphate and those of sodium, potassium, and calcium, (3) the very complex compounds known as proteins. A protein is a colloid substance consisting of carbon, hydrogen, oxygen, and nitrogen, with sometimes small quantities of sulphur and phosphorus. A familiar example is the albumen which, mixed with water, forms white of egg. Proteins are very complex chains of amino acids, that is, compounds which contain both the basic radicle —NH_2 and the acid group —COOH, so that they can combine with each other through the peptide link,



A simple example is aminoacetic acid or glycine, $CH_2.NH_2.COOH$. There are some twenty amino acids, and the nature of a protein depends not only on which of these are present in its molecule, but on the order in which they are arranged in the chain. The proteins of the body are many, and even those of similar parts in different animals are slightly different. That the food does not consist of proteins identical with those of the body it is entering does not matter, since in digestion proteins are resolved into the amino acids of which they are composed and the animal so recombines these as to meet its own needs. The food must, however, supply the right amino acids in sufficient quantities. It is found, for instance, that mice fed upon a diet in which the only protein present is zein, the protein of maize, which does not contain the important constituent tryptophan, are unable to support life. Proteins are important in the food of all animals, because, while, like other substances that we shall mention below, they can be oxidised to provide energy, it is normally they alone that can make good the protein matter that every living body contains and loses by wear and tear and also that can provide such material for growth. When they are to be used for fuel the nitrogen is discharged from their molecules as ammonia. This is deamination; it is the ultimate source of most of the nitrogenous compounds which are mentioned below as forming part of the excreta.

Besides these substances the food usually contains (4) carbohydrates (sugars, starches, and related substances) which are cyclic polyhydric alcohols, but may contain ketone or aldehyde groups as well, (5) fats, which are esters of long-chain acids. It is chiefly these two classes of substances that are oxidised to provide energy. Both contain carbon, hydrogen, and oxygen. In carbohydrates the oxygen is present in exactly the proportions to oxidise the hydrogen, as in cane sugar and malt sugar or maltose, which both have the formula $C_{12}H_{22}O_{11}$, grape sugar or glucose, $C_6H_{12}O_6$, and starch $(C_6H_{10}O_5)n$. In fats there is relatively less oxygen; therefore they require for complete combustion more of that element than is needed to oxidise the carbon, and their potential energy is greater than that of carbohydrates. In digestion, insoluble carbohydrates, such as starch, are dissolved by conversion into glucose or other simple sugars, and fats are partially split into soluble components—fatty acids and glycerol.

Both these processes, and also the digestion of protein, are

hydrolyses—decompositions into smaller molecules with the aid of water taken up. Thus :

$$\underset{\text{(Starch)}}{2(C_6H_{10}O_5)n} + nH_2O = \underset{\text{(Maltose)}}{nC_{12}H_{22}O_{11}}$$

$$\underset{\text{(Maltose)}}{C_{12}H_{22}O_{11}} + H_2O = \underset{\text{(Glucose)}}{2C_6H_{12}O_6}$$

and again :

$$\underset{\text{(the fat Stearin)}}{(C_{17}H_{35}COO)_3C_3H_5} + 3H_2O = \underset{\text{(Stearic acid)}}{3C_{17}H_{35}COOH} + \underset{\text{(Glycerol)}}{C_3H_5(OH)_3}$$

They are all initiated by organic substances called enzymes, which take part in the reaction but are restored at the end. Enzymes are usually named by the addition of the suffix *-ase* to the name of the substrate on which they act.

Since proteins, carbohydrates, and fats are among the compounds known as 'organic', which, in nature, are found only in the bodies of plants and animals and in their remains, such bodies are a necessary part, and the chief part, of the food of all animals. From the same source animals must also obtain (6) other organic substances needed in small quantities. These include the vitamins. These substances, originally manufactured by plants, are transmitted to herbivorous animals, and so to the carnivores, and though needed in very small quantities, are essential to life. When, for instance, young rats are fed upon an artificial liquid containing the protein, sugar, and fat of milk in the usual proportions, they fail to grow, but the addition to their diet of a very small quantity of fresh milk (which contains the vitamins) causes them to grow in a normal manner (Fig. 1.5). The structure and mode of action of many vitamins are now known. They are nearly all required to enable some particular reaction to go on ; thus of the B-vitamins

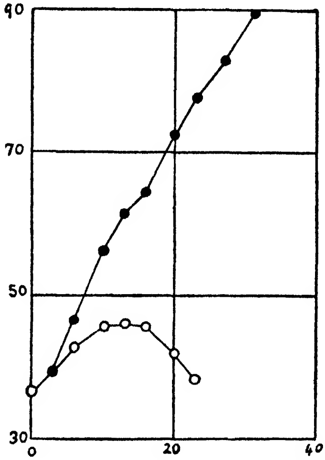


FIG. 1.5.—Curves showing the effect of vitamins on the growth of rats.—From Hopkins.

Lower curve (white circles), rats fed on artificial milk alone. Upper curve (black circles), rats fed on artificial milk and 2 ml. of cow's milk daily. Average weight in grammes, vertical. Time in days, horizontal.

thiamine is necessary for the oxidation of pyruvic acid and α-ketoglutaric acid.

The digested materials undergo absorption into the substance of the body, leaving the indigestible matter to be cast away as the dung or fæces. Incorporation, however, is not brought about simply by the absorption of digested matter. Neither before nor after digestion is the food of the same composition as the substance to which it is to be added. The flesh of a dead ox or sheep differs considerably in composition from that of a living man, and the difference is increased by its digestion. In the course of incorporation the food has therefore to undergo chemical changes by which it is converted into the substances which compose the body, and these changes it undergoes by the activity of the living matter itself. That is to say, the living substance has the power of making, out of unlike materials, additional matter of its own composition. The process by which this is done is known as assimilation. Both absorption and assimilation are processes in which work is done, and therefore involve the use of energy, but their net result is to add to the amount of material composed of complex molecules, and therefore to the amount of energy, in the body.

PROVISION OF ENERGY: RESPIRATION

In all chemical reactions energy is either set free, in which case the reaction is said to be exergonic, or absorbed from the environment, when the reaction is called endergonic; since most of the energy usually appears as heat, leading to either a rise or a fall in temperature, it is usual to speak of the two kinds as exothermic and endothermic respectively. Animals obtain their energy from exothermic chemical processes most of which are oxidations of proteins, carbohydrates or fats. Much of this oxidation does not need free oxygen, and is called anærobic; it consists of the removal of hydrogen to a substance called a hydrogen acceptor, the chief of which are derivatives of the B-vitamins riboflavin and nicotinamide. The final stages, in which molecular oxygen from the air or dissolved in water is used, lead to a complete oxidation of carbohydrate and fat to carbon dioxide and water. Proteins also give these two compounds, but their nitrogen and some of their hydrogen are never completely oxidised, and appear, as we have seen, as ammonia. Almost all animal tissues

can live anærobically for a time, and it is possible that some animals, living in environments such as the mud of lakes and the hind-gut of other animals, can live their whole lives without oxygen and are completely anærobic.

The provision of oxygen and the removal of carbon dioxide are known as respiration. For the whole series of processes leading to the provision of energy no single term exists, although ' respiration ' has sometimes been extended, with various qualifications, to cover either all of it or those types of it that need oxygen.

EXCRETION

The waste products of the provision of energy, of which carbon dioxide and ammonia are the chief, and any other useless substances formed by chemical reactions in the body, must be eliminated, a process known as excretion. The ammonia may first be changed to other less active substances, such as urea and uric acid.

TYPES OF ENERGY: METABOLISM

The energy of animals appears in various forms. The most characteristic and important of these are contraction, chemical work, excretion, secretion, and the conduction of impulses. Contraction is the process by which mechanical movements are carried out, whether they are obvious and external, as in walking and swimming, or internal as in the beating of the heart. In it a portion of the living substance changes in shape but not in size, growing shorter in one direction but thicker in others. This may easily be felt in the working of any of the great muscles of the human body, as when the well-known biceps, in shortening to pull up the forearm, grows at the same time thicker. It should be noted that the opposite of contraction, as used in this sense, is not expansion but relaxation. Instances of chemical activity are seen in the building up of one substance of the body in growth, in the laying down of food reserves such as the glycogen of the liver, and in the formation of the constituents of the many juices which are used for various purposes in the body. Thus the gastric juice, by which food is digested and disinfected in the stomach, contains among other substances hydrochloric acid, whose formation in the face of the alkalinity of the blood involves very

considerable chemical work. Excretion and secretion both involve, in addition to chemical activity, the transference of substances across membranes. Where this is in the direction of the concentration gradient, and exceptionally otherwise, it needs no energy, but more often work has to be done if it is to take place. Thus the removal of the waste products from the blood so that they can be eliminated as urine needs energy, which is provided chiefly by the heart beat ; the rest, and all that required for the secretion of such things as gastric juice, comes from chemical processes taking place at the site of the transfer. The conduction of the nervous impulse depends in part on the transfer of ions and chemical substances across the cell membrane, and so is akin to secretion, but it includes also electrical changes.

These types of energy appear in almost all animals, but there are others of more restricted distribution. Thus in man and the other warm-blooded animals much of the energy is deliberately produced as heat to maintain the body temperature, in the glow-worm energy appears as light, in many vertebrates and insects as sound, and in a few animals, such as the electric eel, as powerful electric potentials.

Chemical changes that lead to the building-up of the body are called anabolism ; those that lead to its disintegration and to the provision of free energy are called katabolism. The two together are metabolism.

THE STRUCTURE OF LIVING MATTER

The characteristics of living matter with which we have dealt so far have been functional, that is, they have been concerned with processes or actions, but there are also others which are structural, or concerned with the form which living matter takes. The first is that living bodies always contain the substance known as protoplasm ; in fact most of the processes characteristic of life go on only in the protoplasmic parts, the others being by comparison lifeless. Protoplasm will be considered in more detail later, but it may be said here that it is an aqueous solution in which protein is the most important constituent. The other parts of the body are formed material, made by the protoplasm ; an example is the ground substance of bone (Fig. 26.13), consisting largely of salts of lime, to which it owes its hardness.

The second structural feature of living matter is that it possesses

a considerable degree of organisation. In many animals, as we shall see in a later chapter, the protoplasm is not continuous, but is arranged in a number of minute units known as cells (Fig. 1.6). In each cell a small protoplasmic body, the nucleus, acts as a regulative centre, and on the surface the protoplasm is modified to form a cell wall. If the protoplasm is not divided into cells, nuclei are still present.

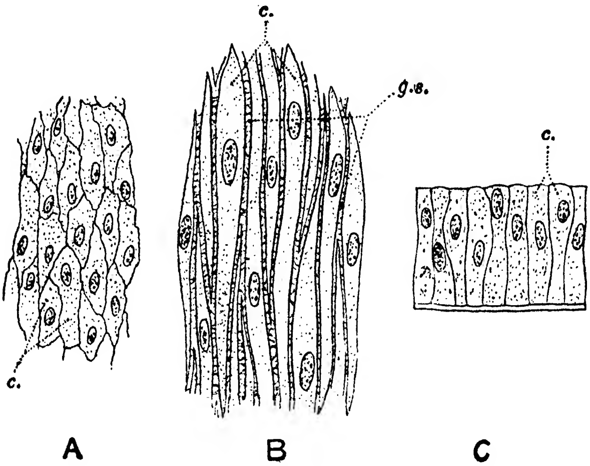


FIG. 1.6.—Portions of animal tissues, highly magnified, to show cells.

A, The lining of an artery ; *B*, muscular tissue from the wall of the intestine ; *C*, the lining of the intestine. *A* and *B* are shown in surface view, *C* in section.
c., Cells ; *g.s.*, ground or intercellular substance, traversed by threads of protoplasm from cell to cell.

ORGANS

Apart from the microscopic division of its protoplasm, the living body consists of a number of parts each of which does a particular portion of the work of the whole. Such parts are called organs. Thus animals may have sense organs, such as the eyes and ears, for the reception of stimuli ; nervous organs, forming a nervous system (usually provided with a central station such as the brain), for the conduction of impulses set up by these and other stimuli, to the organs which carry out the main part of the reaction ; locomotive organs, such as legs and wings and fins, to carry the body towards food or from danger ; organs of offence and defence, such as teeth and claws, for procuring food and resisting attack ; organs of digestion, such as the stomach and

bowels ; organs of circulation, such as the heart and blood vessels, which distribute digested food, carry waste matters to the excretory organs, such as the kidneys, and gases to and from organs of respiration, such as lungs and gills, and transport materials in general ; and organs of reproduction. An organ may consist of subsidiary organs. Thus the leg is supported by skeletal organs known as bones, moved by muscles, and served by blood vessels and nerves. A complex of parts which work together is known as an organism, and this name is often applied to animals and to plants, for plants also are provided with organs, and are alive. The provision of separate organs for particular functions is called organisation or differentiation ; the assignment of particular functions to separate organs is called, by analogy with the similar separation of functions in modern industry, the division of physiological labour. This exists to a very various extent among animals, and of two animals that which has the larger number of different organs is said to be the more highly organised or more highly differentiated, or simply the higher, though this last word is also used in a slightly different sense in connection with the theory of evolution (Chap. 30). The higher the organism, the greater is its efficiency in coping with its surroundings, the greater the vicissitudes in them which it can survive. There are also great differences in form between the organs of animals of the same grade of organisation. Thus a butterfly is as highly organised as a fish, but its organs are utterly different in form. The differences in structure between animals may correspond to differences in their modes of life. Many animals which live in water have, for instance, very different organs of locomotion and respiration from those which live on land ; the sense organs of an internal parasite are much less highly differentiated than those of an animal which has to seek food and avoid enemies from hour to hour ; and a carnivorous animal has organs for seizing and eating its food which are different from those of one whose diet is vegetarian. This correspondence between organisation and mode of life is known as adaptation.

TISSUES

Organisation involves more than the mere localising of functions —more, that is, than the existence in the body of regions where special functions are performed. It involves also a specialisation

of each of these regions to fit it for its special functions. This specialisation is found partly in the shape of each organ, but also largely in its texture and composition. The substance of the body is not alike throughout, but different portions of it have differences in texture and chemical composition which confer upon them different properties. Thus the outer layer of the skin is firm and hard to penetrate, bone is rigid, blood is fluid, the substance known as connective tissue is tough and binds other tissues together, nerve has the power of conduction highly developed, and muscle that of contraction, and so forth. Such a portion of the body-substance with particular properties, due to a particular texture and composition, is known as a tissue. An organ may consist of one tissue throughout, but is usually built up of several, upon the nature and arrangement of which its powers depend. Thus a muscle contains, besides muscular tissue, connective tissue to bind it together and nervous tissue to conduct through it the impulses which cause it to contract.

CO-ORDINATION

Many of the processes which go on in living organisms lead to action upon the outer world, but others are directed only to keeping the machine in condition. The needs of the several organs in the way of food, oxygen, and the removal of waste, are very different, and vary from time to time with the activity of the organ. Often, too, the activity of one organ must be accompanied by an increase or depression of that of some other organ, as when heavy work by muscles calls for a release by the liver of fuel in the form of sugar, or in an active gland or muscle the walls of the blood vessels relax their contraction and so allow a better flow of blood through the working tissue. Again, in growth the formation of the various parts of the body needs very strict adjustment. In all such respects the processes of the body are subject to co-ordination. This is effected in animals by the two systems of communication within the body—the blood vessels or other transporting system, and the nervous system.

Substances secreted into the blood by various organs affect the working of other organs which they reach in the course of the circulation. Some of these substances are not produced *ad hoc*. Thus the carbon dioxide passed into the blood by active organs as a result of the oxidation going on within them alters the degree

of acidity or alkalinity of the blood, and this regulates the quantity and quality of man's blood supply, the acidity causing small local blood vessels to dilate, so that the active organs are flushed with the blood they need, and stimulating the part of the brain which governs respiration, so that rapid breathing oxygenates the blood and removes the excess of carbon dioxide. The vertebrates, crustaceans and insects, and possibly all animals with a blood system, have also developed special substances, known as hormones, that travel in the blood and affect distant organs. An example is adrenaline, which is discharged into the blood of vertebrates from the adrenal glands in moments of stress. It is carried round in the circulation and tunes up the body for the crisis. It increases the flow of blood in the mucles and brain by quickening the heart beat and constricting the blood vessels of the viscera, augments the supply of fuel for muscular action by causing the liver to pour sugar into the blood, and in other ways prepares the animal for action. The organs that secrete hormones are known as ductless glands or organs of internal secretion.

The other conducting system, the nervous system, is set into regulative action sometimes by the action of the blood upon the central nervous organ, as in the case of breathing mentioned above ; but more often messages sent in along nerves from organs are translated at the centre into outgoing messages to other organs, whose action they regulate appropriately. By them the contraction of muscles, the secretion of glands, the narrowing or dilatation of blood vessels, the beating of the heart, to which the pressure of the blood is due, are all affected, and thus the necessary co-ordination is brought about.

DIFFERENCES BETWEEN ANIMALS AND PLANTS

We have now to observe what are the differences between animals and the members of the other principal division of living beings, the plants. There is no fundamental difference in the composition of the protoplasm which is the essential part of all living things, nor do they differ in the essentials of their life. This will be seen if we compare instances of the activities of plants with those which in the foregoing paragraphs we have drawn from the lives of animals. That the protoplasm of plants is irritable we see in such cases as the turning of a sunflower towards the

sun, or the stimulation by gravity of the stem to grow upward and root downward. That it is automatic appears in such facts as the slow turning of the tendrils of climbing plants till they meet with objects to which they can cling. That it has conductivity can be seen when a stimulus given to the leaf of a mimosa causes distant leaflets to fold. That it can execute movements may in many cases be seen under the microscope, when it will be found to stream round the cell. That it makes substances by chemical activity and secretes them is illustrated by the long list of drugs and other substances obtained from plants. That it grows and reproduces need not be argued. In the sexual reproduction of the higher (or flowering) plants, the part of the sperm is played by bodies produced from the pollen, that of the ova by 'egg-cells' which are contained in the flowers, in organs known as carpels.

For all this agreement in essentials, however, there are between most animals and most plants distinctions which are both far-reaching and obvious. We may take our start from familiar notions on the subject. Anyone who tried to state in words the ideas which he had unconsciously formed of animals and plants would probably find them to be somewhat as follows: An animal is a being that moves and feeds; a plant is a green thing that grows in the earth. Let us examine these notions. It will be best to base our analysis upon our definition of a plant. We find that the information it implicitly contains is: (1) That the plant is green, (2) that it does not swallow food, but draws nourishment from the earth (the fact that it also obtains food from the air is less generally known), (3) that it is fixed in one place and does not move about—usually, indeed, does not move at all.

1. The green colour of plants is due to the presence of the substance known as chlorophyll. This is contained in protoplasmic structures known as chloroplasts, which in the green cells of the higher plants are usually numerous and lens-shaped. Chlorophyll is a mixture of four or more complex compounds of carbon, hydrogen, oxygen, and nitrogen, some of which contain in the molecule an atom of magnesium. It is only found in those parts of plants which are exposed to sunlight, and is never found in multi-cellular animals, except in certain cases where minute green plants live embedded in the transparent protoplasm of animal bodies, as in the green hydra (p. 86). At the same time it

must be remembered that certain plants, such as the Fungi, have no chlorophyll, while many of the simplest animals, the Protozoa, do have it (Chap. 3).

2. More important than the mere presence of chlorophyll is its function in the body, which is connected with the nutrition of the plant. This function is the obtaining of carbon from carbon dioxide by means of the energy of the sun's rays, and the use of it in the manufacture of complex organic substances. Absorbing certain rays of light, the chlorophyll enables the protoplasm to use the energy of the rays to reduce (in the chemical sense) molecules of water and carbon dioxide so that the products can combine to form carbohydrates. This process is known as photosynthesis, and is accompanied by the liberation of oxygen. This can easily be shown in the case of water plants, from whose leaves in sunlight a stream of fine bubbles of oxygen may be seen to ascend. The carbohydrates are used for the formation of various organic substances present in the protoplasm of plants, and in particular of proteins. The nitrogen, sulphur, and phosphorus for this purpose are obtained by the plants as salts in solution in the water which is taken in by their roots, or sometimes, as in seaweeds, by the whole surface of the body. From this peculiarity of nutrition arise several other features peculiar to the life of plants. (i) We have here the reason for the well-known fact that green plants cannot live indefinitely in the dark. (ii) While animals, as we have seen, are always taking in oxygen and giving out carbon dioxide, green plants in the light are continually taking in carbon dioxide and giving out oxygen. Yet it must be remembered that the protoplasm of plants undergoes continually respiration like that of animals, although this is obscured by the reverse process taking place to a greater extent during daylight, and that some animal tissues can assimilate carbon dioxide, though not by photosynthesis. (iii) Though the material included in the protoplasm is similar in the two kinds of organisms, plants manufacture its organic components from simple substances, whereas animals obtain them from other organisms or their products. Therefore, while the food of animals consists of complex organic substances, usually in the state of a solid or liquid protoplasm, and has to be swallowed through an opening, the materials taken in by green plants are simple inorganic substances which can be absorbed as gases or liquids through the surface of the body. It must be noticed, however,

that plants which have no chlorophyll, such as Fungi, and some animals which live as parasites or in decaying matter, absorb their nourishment through the surface of the body, but take it in the form of organic substances, more or less complex, from the living or dead bodies of other organisms.

3. From the mode of nutrition of plants there follows the third character which we have marked in them. In the great

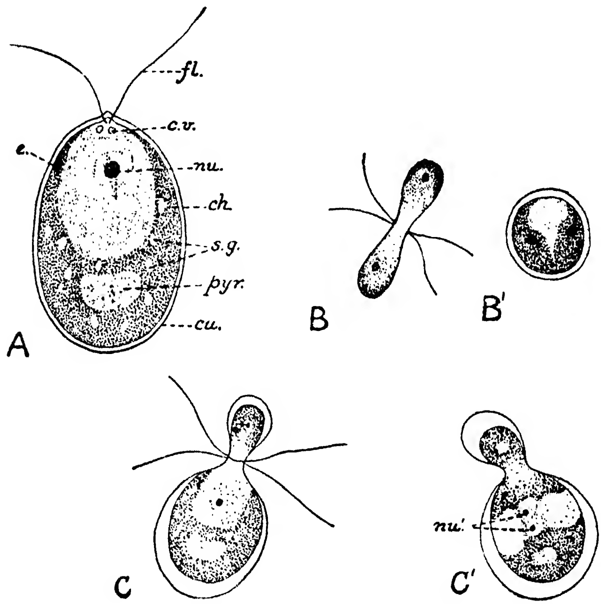


FIG. 1.7.—*Chlamydomonas*, a minute, motile plant.

A, Ordinary individual. B, B′, Two stages in the conjugation of gametes of equal size (isogamy); C, C′, Two stages in the conjugation of gametes of different sizes (anisogamy). The conjugation is 'head on' in each case.

cv., Contractile vacuoles; *ch.*, chloroplast; *cu.*, cuticle of cellulose; *e*, eye spot; *fl.*, flagellum; *nu.*, nucleus; *nu′.*, nuclei of two gametes about to fuse; *pyr.*, pyrenoid (a protoplasmic body which is concerned in starch formation); *s.g.*, starch grains.

majority of animals food must be either sought by locomotion or at least seized by other active movements, as it is, for instance, in a sea-anemone or *Hydra* (Chap. 9). In plants, on the other hand, not only is this necessity absent, but, since it is desirable that they should expose as great a surface as possible to air and water for absorption—as they do, for example, in leaves and roots—the shape of their bodies is necessarily such as to be an actual hindrance to motion. Thus in most plants active motion is restricted or absent, and muscular and nervous tissues are not

found in plant bodies. Certain microscopic aquatic organisms, however, chiefly unicellular Algæ, are exceptions to the rule that locomotion accompanies the animal mode of nutrition only. Though they have one or more chloroplasts and nourish themselves like plants, their body is compact, shaped like an egg or a spindle, and possesses one or more fine lashes of protoplasm (flagella), by the working of which it is rowed or drawn through the water. Many of them, including the example, *Chlamydomonas*, shown in Fig. 1.7, have a pigment spot which absorbs light, and an associated organelle for its appreciation. While some of these unicellular creatures are undoubtedly plants, and others, in spite of their chlorophyll, are best regarded as animals, some, such as *Euglena* (p. 36), are difficult to place. The line between animals and plants, like that between living and non-living, can only be arbitrarily drawn.

4. The necessity for a large surface leads to a fourth character in plants. An extensive surface needs strong support. In correspondence with this need we find in plants a massive skeleton which forms a strong wall to each cell, so that the protoplasm is upheld by an intricate framework of compartments whose walls are thickest in the most woody parts of the body. Owing, no doubt, to the ample supply of starch at the command of the plant, this skeleton usually consists of a modified form of starch known as cellulose. Some groups of plants use other substances, and though cellulose is rare amongst animals it is present in some Protozoa and in tunicates (p. 309).

THE BALANCE OF NATURE

The difference in nutrition between animals and plants has the important result that in their action upon the inorganic world these two kinds of organisms bring about precisely opposite changes, and do so in such a way that each sets up conditions favourable to the activity of the other. The plant, absorbing the energy of the sun's rays, builds up complex organic compounds from simple inorganic substances and in so doing stores chemical potential energy. Though it destroys some organic substances in respiration, the net result of its activity is to increase the stock of them in the world. At the same time it sets free oxygen. The animal, on the other hand, uses as food the substances manufactured by plants, taking them either directly from plant bodies

or after they have been incorporated in a somewhat altered form into the protoplasm of other animals. A rabbit feeding on grass and a stoat feeding on the rabbit and a parasite feeding on the stoat are equally dependent on the plant for their organic food. Such series of dependencies are called food chains. In the protoplasm of the animal these organic substances undergo destruction, in consequence of which there are set free carbon dioxide and simple nitrogen compounds. Thus plants provide food and oxygen for animals, while animals, destroying this food, provide simple nitrogen compounds and carbon dioxide for the use of plants. Since the nitrogen compounds actually produced by animals can mostly not be used by plants, the presence of bacteria is necessary to change them to nitrate, the form in which nitrogen is generally absorbed.

ZOOLOGY: PLAN OF STUDY

Biology comprises botany, which deals with plants, and zoology which deals with animals. Now an organism may be regarded from two points of view according as attention is concentrated upon its structure or its functions, though of course these two are so closely connected that it is impossible to study structure intelligently or function at all without reference to the sister topic. The sciences of zoology and botany are correspondingly divided each into two subordinate sciences, anatomy or morphology, which deals with the structure of the bodies of organisms, and physiology, which deals with their functions. Anatomy is sometimes used as a synonym for morphology, but is often, especially by botanists, taken in a slightly more restricted sense to mean the detailed study of structures, morphology being restricted to general form.

In this book we shall approach zoology chiefly from the anatomical side, partly because our knowledge of the physiology of animals in general is still fragmentary, but chiefly because knowledge of physiology must of necessity be grounded in previous knowledge of anatomy. Wherever possible we shall consider the functions of the structures we find, but we shall avoid imputing imaginary functions to structures which have not been adequately studied. We shall begin with some of the structurally simplest animals, and proceed through the animal

kingdom in what is now generally considered to be an order of increasing complexity. In so doing we shall be following what, according to the hypothesis of organic evolution, is roughly the line which animal life has taken in its temporal development through the ages. Before we consider the evidence for evolution in Chapter 30, we may accept it as a useful working hypothesis, which makes, as it were, a thread on which to hang the discrete beads of our knowledge of particular animals. Of necessity we shall describe and illustrate examples or types, but at the end of each chapter shall consider the more general characters of groups of animals. When we reach the rabbit we shall consider physiology, and also minute anatomy, in rather more detail, and those who prefer may begin with that chapter. Finally, we shall discuss certain topics such as evolution and heredity which concern animals in general.

Proper consideration of the classification of animals must be postponed to a later chapter (p. 715), but something must be said here to explain the terms used in the following pages. Common sense early recognised that animals are not all the same, but that some are alike enough to each other to be included under a common name. Thus all cats are recognisably cats, and are clearly not dogs ; further, cats produce kittens, which in time become cats, while dogs produce puppies which in turn become dogs. To a set of animals distinct enough from all the rest to be called by a separate name, but like enough to each other to be not worth subdividing, the zoologist gives the name species. A set of species with many similarities makes a genus. Genera are collected into families, these into orders, these again into classes, and classes into some dozen or so phyla, which comprise the whole animal kingdom. Occasionally a species is so different from all other species that it has to occupy a genus, a family, or even a class by itself. For convenience in the handling of groups with very large numbers of species, divisions such as super-families and subclasses are interpolated. Families and higher groups are given names which in form are always Latin plurals. Every genus has a name which is a singular Latin noun, and its species are particularised by adding an adjective, also Latin, which agrees in gender with its noun and is called the trivial name, the two together being the specific name. All these except the trivial names are written with capital initial letters, and generic and trivial names are usually italicised. Family names

are usually derived by adding—*idæ* to the root of the name of one of the constituent genera.

We shall frequently refer to sections, which are slices cut across the body so thin that their two sides are the same. If cut at right angles to the fore-and-aft axis of a bilaterally symmetrical animal they are transverse. A section cut vertically along the axis and through the mid-line is called sagittal, one cut similarly but horizontally is frontal. Both these are longitudinal.

2

AMŒBA

THE Protozoa are structurally simpler than other animals in that their bodies are not divided into cells ; each individual consists of a mass of protoplasm with some sort of boundary layer and containing a single nucleus, or occasionally two nuclei or more.

We shall begin with the genus *Amœba*, not because it is really the simplest of Protozoa but because it is easy to observe. There are several species, which agree in a number of points. The protoplasm is divided into a clear outer ectoplasm and an inner granular endoplasm ; there is no secreted cell-wall, but the surface is specialised as a thin plasmalemma, which the electron microscope shows to consist of two membranes, each about 20 Å thick, separated by a less dense layer, the outer membrane being covered by a fringe of fine filaments about 1000 Å long. Both ectoplasm and endoplasm extend into one or more blunt finger-like processes called pseudopodia, the number and size of which are continually changing. One of the largest species is *Amœba proteus* (Fig. 2.2), which is about one-fiftieth of an inch (half a millimetre) across and lives in the mud of ponds, though it is not very common. *A. leschereæ* (Fig. 2.1) is larger and *A. discoides* (Fig. 2.4) smaller, but they are otherwise difficult for the student to distinguish. The following account applies, unless otherwise stated, to all three species. *A. proteus* produces about three or four pseudopodia at a time, all of which are of relatively large size and sub-cylindrical in shape. There is normally one nucleus, which is more or less centrally placed, but about five per cent. of individuals have two, three, or occasionally four nuclei. The nucleus is only just visible in living specimens, but when the animal is killed and stained with certain dyes, the nucleus is conspicuous, since it takes up the colour more deeply than the cytoplasm, and can be seen to be lens-shaped. Just behind the nucleus is a clear spherical space, the contractile vacuole. Besides the granules, the endoplasm contains several small animals or plants which have been taken in as food.

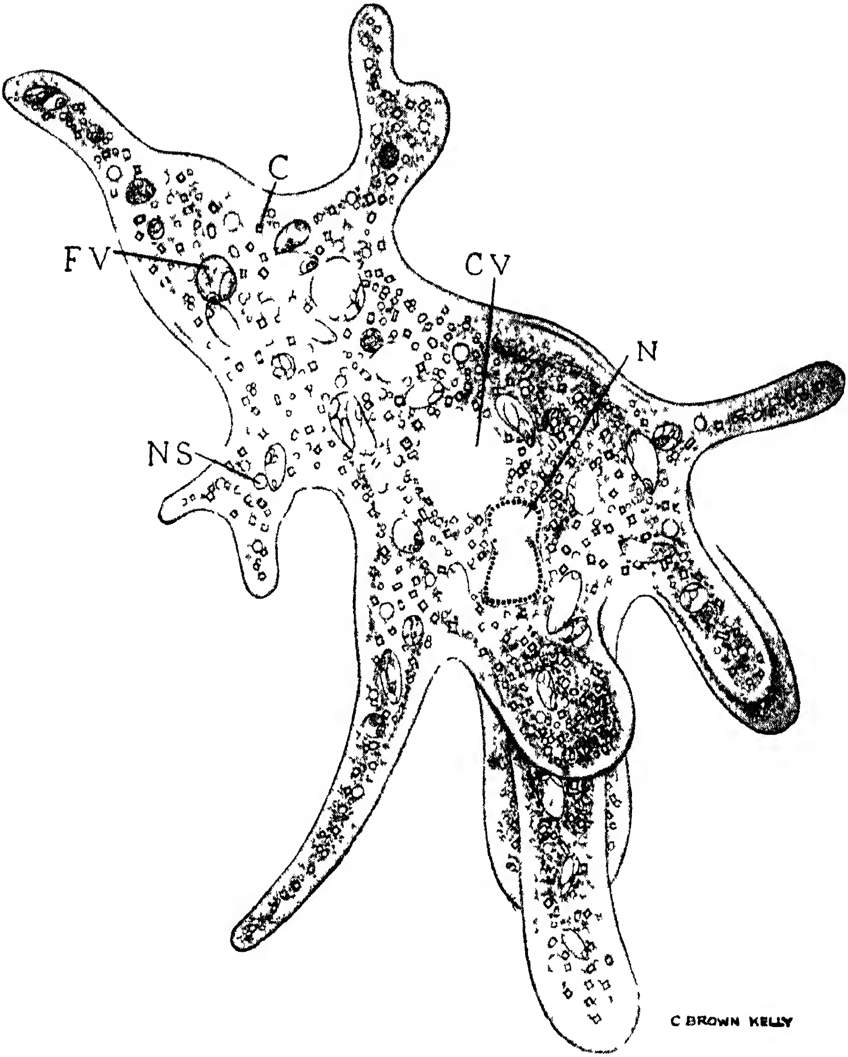


FIG. 2.1.—*Amœba lescheræ.* Drawing of a living individual.—From Taylor and Hayes, *Quart. J. micr. Sci.*, 1944, 84, 295.

C, crystals; *CV*, contractile vacuole; *FV*, food vacuole; *N*, nucleus; *NS*, nutritive sphere. × *c.* 200.

MOVEMENTS

It is common, but incorrect, to describe *Amœba* as shapeless ; in fact each species has a characteristic form, by which it can be recognised, though it is true that there is more variation in that form than is usual in animals. A pseudopodium begins as an out-flowing of the ectoplasm, into which the endoplasm presently flows. The projection grows, and in time so much of the body has

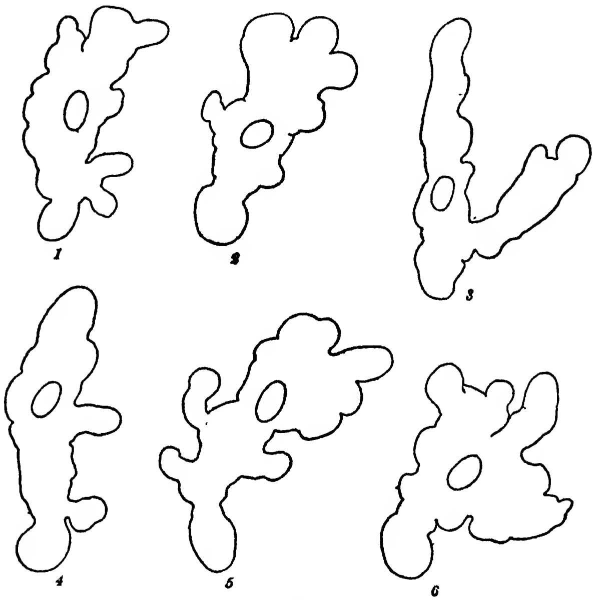


FIG. 2.2.—Successive changes in shape of an individual of *Amœba proteus*, drawn at intervals of two minutes.

moved into it that protoplasm has to be drawn up from behind to take its place, and locomotion has occurred ; this is known as amœboid movement (Fig. 2.2). Subsidiary pseudopodia are formed at the side of the main one, but these are eventually withdrawn. It appears that whatever happens to the amœba, it is always the same end which leads, so that in spite of its apparent irregularity, the animal really has right and left sides. The ectoplasm and the outer part of the endoplasm together form a firm coat, the plasmagel, around the fluid inner endoplasm or plasmasol. It seems that the change of gel to sol liberates energy, which is available for the work of movement. Where a pseudopodium is to be thrust out the plasmagel softens, and the contraction of the

rest of that layer or its conversion to sol at the posterior end, then presses the plasmasol towards this spot, which bulges. As the bulge grows, a covering of plasmagel for its flanks is provided by conversion of plasmasol. The plasmalemma, which is sticky, adheres to the ground where it is in contact, so that the effect of the forward thrusting of the protoplasm within is to roll it along, as an india-rubber bag filled with water may be rolled over a surface, and thus the animal travels in the direction of the thrust. Those pseudopodia of *A. proteus* which do not touch the ground merely protrude without causing locomotion, but the creature may place their tips upon the ground and thus walk upon them. During the movements the contents of the endoplasm—nucleus, food particles, etc.—are carried about freely from place to place in the body, but the contractile vacuole adheres to the inner surface of the ectoplasm and moves with it.

NUTRITION

Amœba feeds on small organisms, which it ingests by surrounding them with pseudopodia, so that the prey, together with a drop of water, is taken into the endoplasm as a food vacuole. This has a wall similar to the plasmalemma, from which it is presumably derived. The prey is killed and digested, the reaction within the vacuole being acid. The chief food of *Amœba* is protein, but *A. proteus* and other species can digest fat. Their ability to deal with carbohydrate is doubtful. The dissolved substances are incorporated, and the undigested parts are egested by the simple process of being left behind as the animal flows along. Different species have different food preferences and *Amœba proteus* does not feed on diatoms but can survive indefinitely on the small ciliate *Colpidium*, which is found in infusions in association with *Paramecium* (p. 45).

Amœba can also take in droplets of protein by the formation of narrow channels in the cytoplasm, from which small vacuoles are pinched off. This is known as pinocytosis, but whether it has any nutritional function is unknown.

IRRITABILITY, AUTOMATISM AND CONDUCTIVITY

The protoplasm of *Amœba* is irritable, automatic, and conductive. Its irritability is not, as in higher animals, localised in sense organs, but that this property exists in it is shown in

various ways. If *Amœba* be stimulated by slight contact or by meeting very dilute solutions of various chemical substances it will form a pseudopodium on the side towards the stimulus. If it be pricked with the end of a fine thread of glass, or come into contact with stronger solutions of chemical substances, it will draw back and flow away. In this case the formation of a pseudopodium in a region of the body other than that which has been stimulated shows that the protoplasm has the property of conductivity. Again, it does not swallow every particle it comes across, but chooses those that either contain nourishing substances or are in motion (in which case they are probably alive and therefore fit for food). By an unkind deception of this ‘ sporting instinct ’, it may be induced to capture and swallow moving particles of glass. It will move away from strong light, but does not appear to perceive a particle of food better in the light than in the dark. All this shows that it receives from foreign bodies various stimuli, and discriminates between them. In contrast to these instances, many of its actions cannot be traced to any stimulus, and must therefore be classed as automatic in the sense in which that word is used in biology. In much of its activity it appears to be exploring its surroundings and to continue on a course until it receives some stimulus which repels it, but sometimes, as in capturing food, it appears to be attracted in the direction from which a stimulus comes.

RESPIRATION AND EXCRETION

Since the pellicle of *Amœba* is thin it is probable that liquid and gaseous substances other than those with very large molecules can pass in and out with some ease, and what evidence there is suggests that this is so. *Amœba* is known to absorb oxygen, and since there are no special organs for the purpose it must be presumed that the gas diffuses in all over the surface. In the same way, since it is virtually certain that no animal can feed on protein without producing nitrogenous waste products, it must be assumed that these diffuse out. Crystals in *A. proteus* and other species have been shown to consist of carbonyl urea, which is presumably an end-product of purine metabolism. In *A. lescheræ* masses of similar crystals have been observed to collect in a large vacuole and, after being violently swirled round, to be shot out.

THE CONTRACTILE VACUOLE

The contractile vacuole can be dissected out, and has an elastic and semipermeable wall similar to that of the cell. Surrounding this are small vesicles which coalesce with one another and burst into the vacuole, so that it gradually increases in size up to a maximum, and then bursts, shedding its clear, watery contents to the exterior ; a new vacuole then grows again in the same spot and the process is repeated. From analogy with the contraction and swelling of the vertebrate heart the small phase is sometimes called systole and the large, diastole. The vacuole removes water, and this is its only known function. The pellicle of *Amœba* has differential permeability for water and for dissolved substances, so, since the osmotic pressure of the cytoplasm is higher than that of fresh water, water must enter osmotically. If this were not eliminated the creature would swell. Marine amœbæ, living in an environment of osmotic pressure approximately the same as that of protoplasm, have no contractile vacuole. The passage of water from the cytoplasm into the contractile vacuole is against the direction of osmotic flow, and must mean that work is being done by the animal. The contractile vacuole is surrounded with mitochondria (Fig. 2.3) which in Metazoa are specially concerned with oxidative processes (p. 501), and in an amœba deprived of oxygen, swelling of the contractile vacuole ceases.

THE NUCLEUS

The nucleus varies somewhat in shape, but in *A. proteus* is usually biconcave. It has a membrane somewhat similar to the plasmalemma, with another much thicker one within. It is

FIG. 2.3.—Electronmicrograph of a mitochondrion of *Amœba*, × 33,000.—From Grimstone, *Biol. Rev.*, 1961. 36, 97.

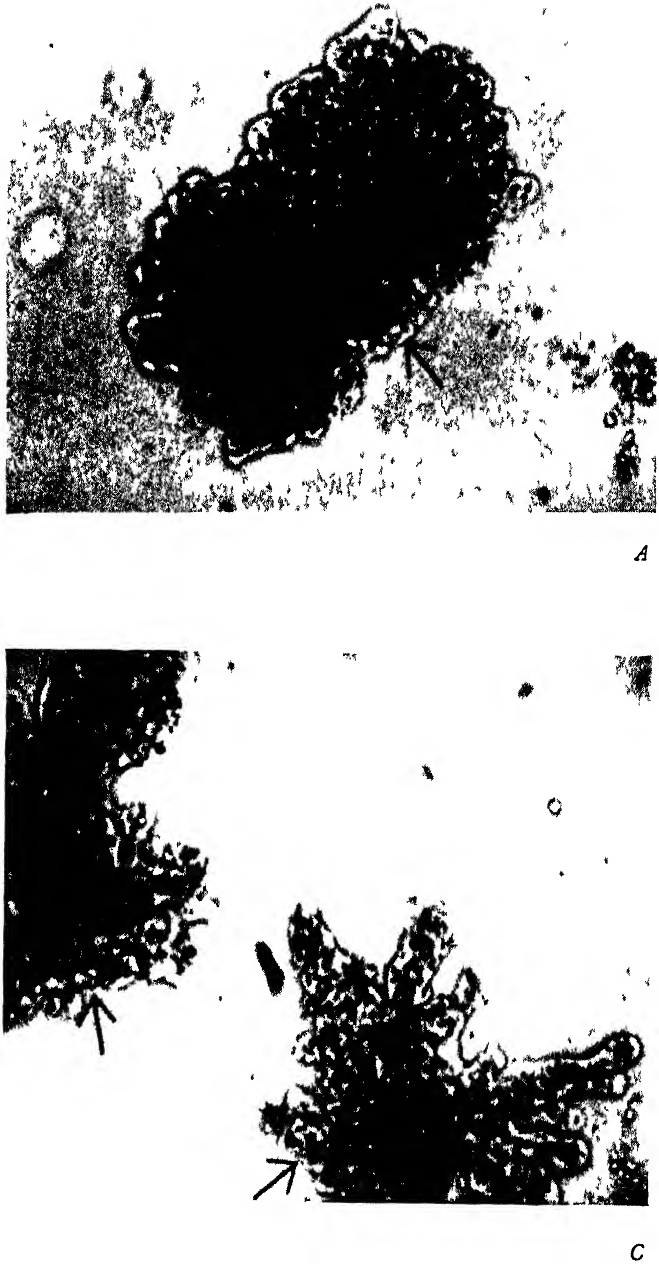
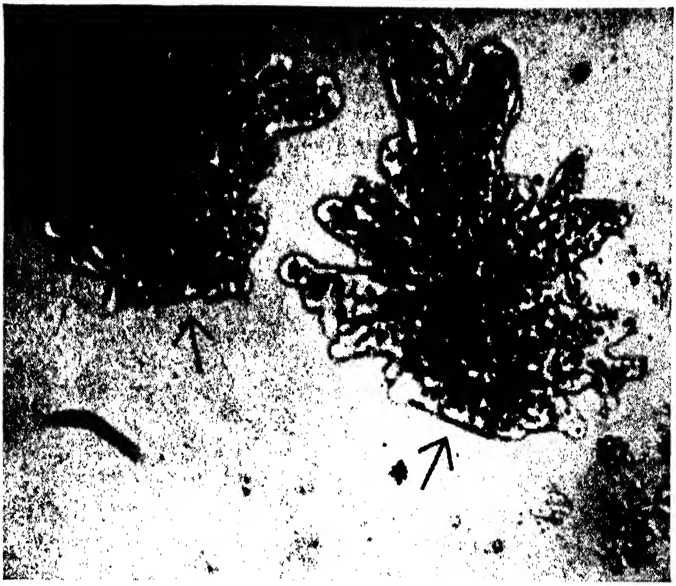
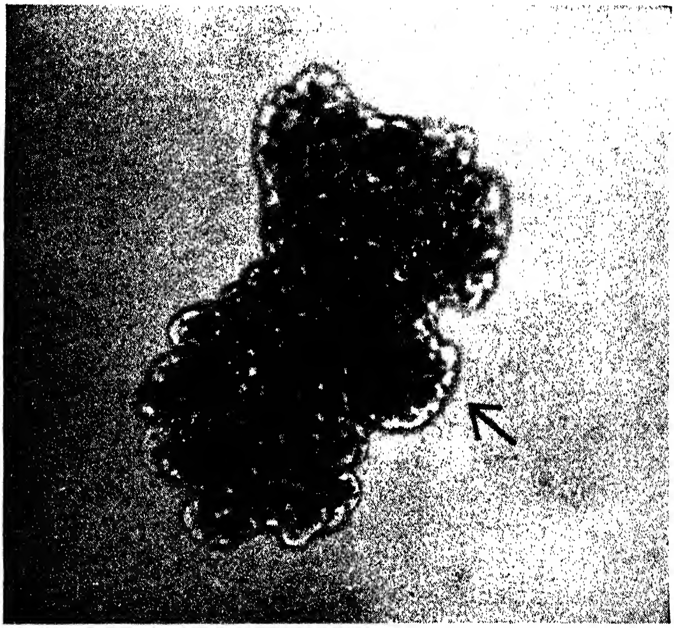


FIG 24 — *Amœba discoides* *A–C*, stills from a cinematograph film of a dividing animal   the arrows indicate the tail, which always remains posterior in



B



D

locomotion. *D*. a photomicrograph of another individual showing the tail more prominently. × *c*. 400. (Photographed by Dr. R. J. Goldacre.)

possible in various ways,, to remove the nucleus from *Amœba proteus*. Individuals thus amputated continue living for some days, and then die. They can move, but their pseudopodia are fewer and unusual in shape ; they can injest and kill small prey, but cannot digest it ; they give normal responses to stimuli, but their oxygen consumption is greatly reduced. All this suggests that the nucleus is in some way responsible for the formation or activity of enzymes. Unfavourable conditions of life may bring about a condition known as depression, in which the nucleus of the amœba is enlarged and the various functions become deranged

LIFE-HISTORY AND REPRODUCTION

The every-day reproduction of *Amœba* is by a process known as binary fission, in which first the nucleus and then the cytoplasm parts asunder into two halves, each of which appears to differ from the parent in nothing but size. The division of the nucleus is generally considered to be a modified mitosis (p. 696). Spindle-fibres, both polar and inter-zonal, are apparent, and at metaphase there appear across the equator very many granules of chromatin, which are formed out of the clear centre of the nucleus. They move to the poles in anaphase, but their division has not been clearly made out. The nuclear membrane persists throughout metaphase, but possibly shatters for a brief period during anaphase. After the division of the nucleus the cytoplasm flows apart into two bodies, each of which contains one of the daughter nuclei, which become fully restored to the resting condition about five hours after the cytoplasm divides. The new cells are in some species connected at first by a bridge of protoplasm, but this becomes narrower until it breaks through and two new individuals come into being, the whole process having taken about one hour. The part where the break occurs becomes the ' tail ' of each daughter amœba, and is always posterior as the animal moves (Fig. 2.4).

There is much dispute as to whether *Amœba* has other methods of reproduction. Some authors have maintained that it can live ' indefinitely ' with nothing but binary fission, but this word has sometimes been used for experiments lasting only a few months. Other authors have maintained that binary fission can continue only if conditions are good, and that if they become adverse a process of spore-formation, with or without encystment, supervenes. According to one of the best accounts, binary fission occurs

in what may be called the adolescent stage of a culture so long as conditions are suitable. When the culture is mature and a change in the environment occurs, multiple fission or spore formation takes place.

The nucleus divides till a very large number of small nuclei has been formed. These pass to the surface of the cytoplasm, which gathers into a little mass around each of them to make spores, which break free, feed for a week, and then encyst. After a week or more they emerge, feed and grow, and then encyst again for up to a month. This process is repeated, and after three months the amœbæ, which are now seven times the diameter of the original spores, emerge from the cysts and grow rapidly to the adult size.

The sceptics believe that these spores are other organisms with which the culture is contaminated, and that adverse conditions are met by the survival of a few hardy but otherwise normal individuals, which seems, in terms of natural selection, to be most unlikely.

Some authors have claimed that *Amœba* meets adverse conditions by withdrawing its pseudopodia and secreting round itself a tough case or cyst, but others have failed to find such stages. If they occur they presumably enable the amœba, as do the cysts of other animals, to survive drying because their activity, and hence their respiration, is negligible.

Syngamy has been described for a number of species of *Amœba* by a few authors, but is not generally accepted. A peculiar process known as plastogamy, well known in some other Protozoa, has also been described. In this the cytoplasm of several individuals fuses, forming a single mass which contains several nuclei. A multinucleate body formed in this way is called a plasmodium. Quite another kind, called a cœnocyte or symplast, is found in some species of *Amœba* and in the related *Pelomyxa,* where nuclear division takes place one or more times without division of the cytoplasm. Plasmodia and symplasts differ only in their mode of formation and are collectively known as syncytia.

3

FLAGELLATE PROTOZOA

POLYTOMA

WATER in which organic matter is decaying always contains numerous small organisms of various kinds. Among these, when decomposition is well advanced, there can be found with the aid of the microscope minute, colourless organisms of a species known as *Polytoma uvella* (Fig. 3.1), which feed by absorbing from the water through the surface of their bodies substances in solution derived from the decaying matter. The body of a *Polytoma* is an egg-shaped mass of protoplasm without any internal skeleton. A pair of long protoplasmic lashes or flagella project from one end, and by the lashing of these it swims with a somewhat jerky course, the end at which the flagella are placed being forward. The permanent shape of the body is due to a thin cuticle; that is, not to a surface layer of the protoplasm, but to a protective covering formed by secretion. It is pierced by two pores for the flagella. Two contractile vacuoles lie close behind the flagella and contract alternately. There is one nucleus, placed somewhat behind the middle, and there is sometimes a spot of red pigment situated in the front part of the body. The hinder region contains numerous starch granules. These must be formed by the protoplasm from substances absorbed in the food: they serve as a reserve of nutriment, and are used up during starvation. Their presence is interesting, for starch, though it is common in plants, is rare in the protoplasm of animals, which, if they store carbohydrates, usually do so in the form of glycogen. They suggest that *Polytoma* is at least closely related to plants. It is, to all intents and purposes, a colourless *Chlamydomonas*, an organism which is clearly a unicellular alga. Like animals, *Polytoma uvella* needs

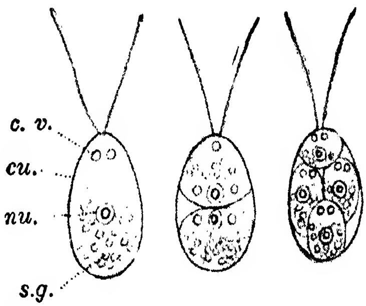


FIG. 3.1.—*Polytoma uvella*: three stages in ordinary fission. *c.v.*, Contractile vacuole; *cu.*, cuticle; *nu.*, nucleus; *s.g.*, starch grains.

an organic source of carbon, but like plants it can exist on inorganic nitrogen. *Polytoma* can encyst, and in the encysted state is carried about in dust, etc., to germinate in favourable circumstances elsewhere.

REPRODUCTION

Reproduction is usually brought about by a process known as repeated fission, in which binary fission is repeated so as to form four daughters before the young separate, but sometimes there are only two offspring. Fission takes place within the cuticle, this being carried about during the process by the action of the flagella, which remain attached to one of the daughters. The flagella are then withdrawn, each daughter forms two small flagella, and the cuticle of the parent is dissolved. At intervals of a few days syngamy takes place. Two ordinary individuals come together and fuse, their nuclei joining and their cytoplasm flowing into one mass, which then encysts. After a resting period the zygote divides by repeated fission into eight, each of the daughters grows two flagella, and the cyst is dissolved. In regard to this process we must notice : (1) that syngamy can occur at any time in the life of the individual, and does not take place between special germ cells which cannot develop without it : in most animals, on the other hand, syngamy is obviously impossible in the adult and can only take place between the germ cells before they develop the rest of the body ; (2) that the gametes are alike, and not, as in most animals, of two kinds, a passive kind, which bears the bulk of the cytoplasm, and an active kind, by which is carried out the locomotion which the process involves. Both gametes in *Polytoma* are fairly well supplied with cytoplasm and both are motile. Only when one is older than the other is there sometimes a difference in size.

The syngamy of two like gametes, whether they be ordinary or special individuals, is known as isogamy ; syngamy of unlike gametes is anisogamy ; if, as in most animals, they differ not only in size but also in that the larger is passive and the smaller active, the process is known as oögamy.

In *Chlamydomonas* (Fig. 1.7) syngamy takes place between special small forms which arise by repeated fission of the ordinary forms. These special gametes, however, are like the ordinary individuals in all but size.

EUGLENA

The many species of the genus *Euglena* (Fig. 3.2), often so common in puddles as to give them a green colour, are flagellate organisms mostly about 50 to 60 μ long. The front end is blunt and bears one flagellum rooted at the base of a funnel-shaped pit, formerly known as the gullet but now as the reservoir. Both names are misleading, since the prevailing opinion is that it is used neither

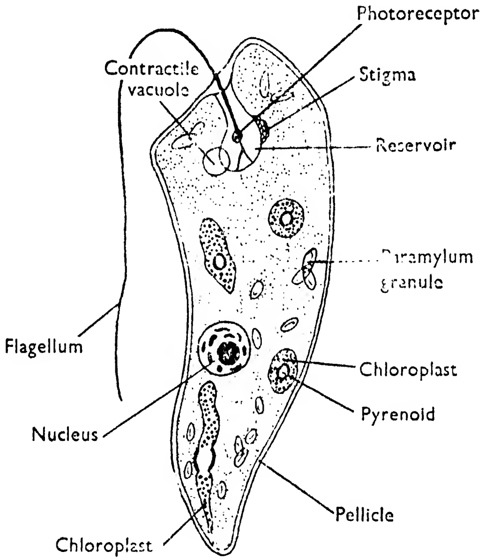


FIG. 3.2.—*Euglena gracilis*. × 1,250.—After Mackinnon and Hawes, *Introduction to the Study of the Protozoa*, 1961. Clarendon Press, Oxford.

for taking in food nor for storage. The base of the flagellum appears to bifurcate but it is probable that there is really a second short flagellum, since each limb has its own basal body in the cytoplasm, and some related species clearly have two flagella of which one is shorter than the other. The electron microscope shows that the flagellum bears a row of filaments, some five or six times its diameter in length. There is a strong pellicle, a distinct ectoplasm, and a central, spherical nucleus. The green chloroplasts (p. 17) vary in shape and number with the species; each usually contains a pyrenoid in which the starch-like substance paramylum accumulates. The body changes its shape by

slow waves of contraction (Fig. 3.3). There is a large contractile vacuole which discharges into the expanded base of the reservoir. Just before the collapse a number of small vacuoles appear near the old one, and these coalesce to form a new vacuole (Fig. 3.4).

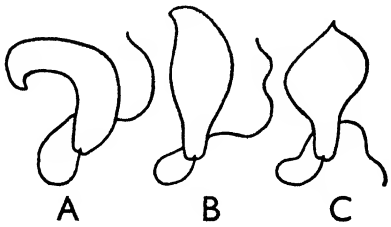


FIG. 3.3.—*Euglena viridis.*
A, *B*, *C*, Three postures of the body.

A red pigment spot or stigma lies against the front side of the reservoir and, probably by casting its shadow on a swelling near the base of the flagellum, causes the animal to turn until it is swimming either toward or away from one source of light, the only positions in which the swelling is uniformly illuminated. Reproduction is by binary fission, beginning at the front end,

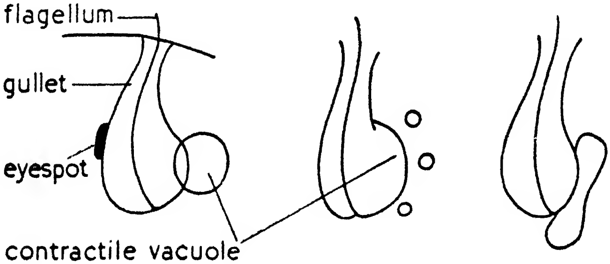


FIG. 3.4.—Stages in the formation and discharge of the contractile vacuole in *Phacus*, a flagellate related to *Euglena*.—Modified from Hyman, *The Invertebrates: Protozoa through Ctenophora*, by kind permission of McGraw-Hill Book Company.

the nucleus undergoing a peculiar mitosis in which there is no division centre. The basal body divides, one half going with the old flagellum, to one daughter, the other growing a new flagellum. In some species fission takes place also in a cyst. The occurrence of syngamy is extremely doubtful. Our knowledge of the nutrition of *Euglena* is too confused and complicated to be summarised in an elementary book. It is doubtful if *E. viridis* can feed in an

entirely plant-like manner, though *E. gracilis* can. All species can grow if they are in the light, provided that a suitable source of organic nitrogen be present, and some can also grow in the dark if organic carbon and nitrogen be available; under these circumstances the chloroplasts lose their green colour.

PERANEMA

Peranema, common in stagnant water, is a colourless relation of *Euglena*. It is pear-shaped at rest but very active in changing its shape, and has two flagella, of which only one is free, while the other is attached for most of its length to the outside of the cell. It feeds by swallowing smaller organisms into a cytostome, the wall of which bears two stiff rods which can pierce and grip animals as large as *Euglena*. The morphology of the cytostome is disputed, some authors saying that food vacuoles are formed at the base of the reservoir into which the flagella project, others that there is a separate channel opening into the reservoir near its outer end, and some that the cytostome and reservoir are completely separate. Probably *Peranema* is also saprophytic (see below).

CHOANOFLAGELLATA

The choanoflagellates have a bell-shaped body attached by a stalk at one end, and at the other there is a single flagellum surrounded at its base by a peculiar collar of protoplasm inside which particles of food are absorbed (Fig. 3.5). The body of some species is nearly surrounded by a secreted cap-shaped case, and in others the stalks of several individuals are joined to make a colony.

NUTRITION AND FLAGELLA

The organisms which we have been discussing in this chapter exhibit all the three types of nutrition practised by animals and plants. In *Chlamydomonas* simple inorganic substances are absorbed through the surface, and from them complex substances are manufactured by means of the energy of the sun's rays. Such organisms are said to be holophytic. In *Copromonas* and *Peranema* complex organic substances are taken in through a

mouth, after the manner of animals. Such organisms are said to be holozoic. In *Polytoma*, organic substances are absorbed in solution through the surface of the body. Such organisms are said to be saprophytic if they are plants, or saprozoic if they are animals. The substances which form the food of various saprophytic organisms differ a great deal. In *Polytoma* they are

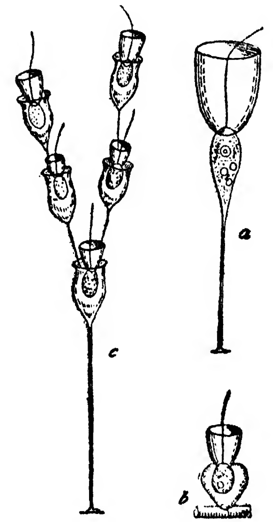


FIG. 3.5.—Choanoflagellata.
a, *Monosiga*; *b*, *Salpingœca*; *c*, *Polyœca*.

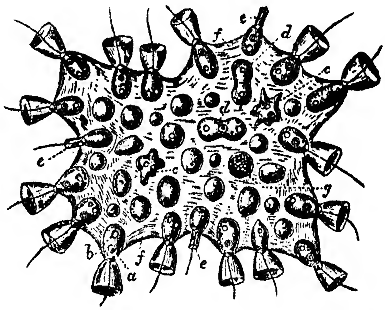


FIG. 3.6. Choanoflagellata: *Proterospongia*.
a, Nucleus of a collared member of the colony; *b*, contractile vacuole; *c*, amœboid member; *d*, division of amœboid member; *e*, flagellate member with collar contracted; *f*, jelly; *g*, member forming spores.

relatively simple (acetates, etc.), but many parasites in the alimentary canals of animals nourish themselves saprozoically on the digested food of their holozoic hosts.

Flagella and cilia have been shown by the electron microscope to have a remarkable uniformity of internal structure. A sheath surrounds a clear space, in which is a circle of nine fibres, and within this a central pair surrounded by a sheath. Between each outer fibre and the central pair is a smaller fibre. Each outer fibre appears in section like a figure ∞ with arms, and as the arms are directed tangentially to the flagella the latter has no axis of symmetry (Fig. 3.7). The outer fibres continue into the cytoplasm to form a basal body or kinetosome, but each becomes here a triple, instead of a double, circle. Sometimes the fibres in the basal granule are joined by rays (Fig. 3.8).

FIG. 3.7.—Electronmicrograph of flagella of *Trichonympha* in transverse section. × 130,000.—From Grimstone, *Biol. Rev.*, 1961. 36, 97.

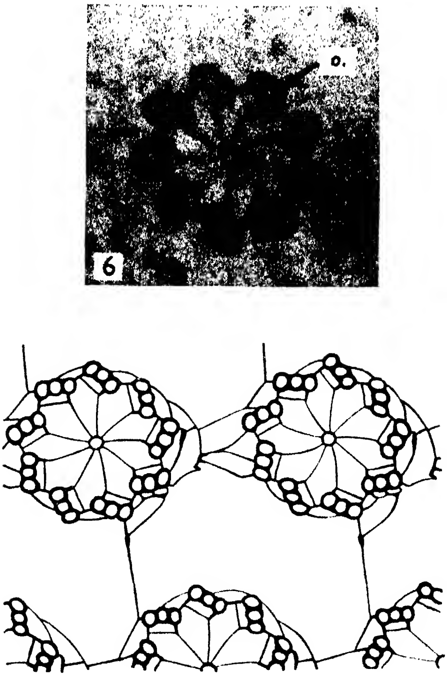


FIG. 3.8.—The basal body of *Trichonympha*. A, an electronmicrograph of a transverse section, × 130,000. *o*, the 9 triplet outer fibres ; B, a diagram based on similar electronmicrographs.—From Grimstone, *Biol. Rev.*, 1961. 36, 97.

4

MONOCYSTIS

AMONG the organs of reproduction of an earthworm are certain sacs, known as the seminal vesicles, in which the sperms ripen. Here are generally to be found specimens of the parasites known as *Monocystis* (Fig. 4.1), which live by absorbing, through the surface of their body, the fluid in the vesicles which is intended for the nourishment of the spermatozoa. Many species may be

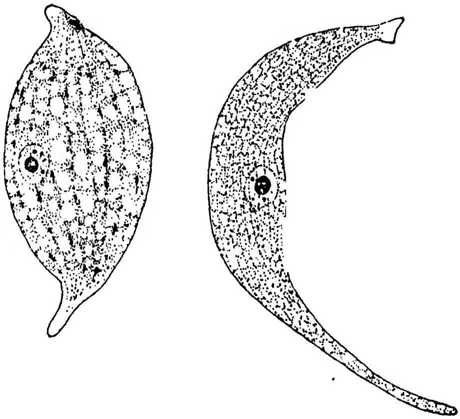


FIG. 4.1.—*Monocystis agilis*. Stout and slim forms of the trophozoite (after Hesse). × 200.—From Mackinnon and Hawes, *An Introduction to the Study of the Protozoa*, 1961. Clarendon Press, Oxford.

present. The large *M. magna*, now known as *Nematocystis magna*, is easily visible to the naked eye as white threads, hanging by one end from the funnels of the vasa deferentia (see p. 173) and is found only in *Lumbricus terrestris*. *M. agilis*, the commonest species in Great Britain, and *M. lumbrici*, the first species to be described, are smaller and are more often found free in the fluid among the developing spermatozoa of several species of worm. The body of a full-grown *Monocystis* is long and narrow, and consists of a soft, granular endoplasm and a firm, clear ectoplasm. The endoplasm contains numerous granules, many of which consist of the carbohydrate substance paraglycogen, and the ectoplasm is covered with a stout cuticle and has in its deeper layer a network of threads, the myonemes, which are possibly contractile, since slow waves of contraction occasionally pass along

the body. In the endoplasm there is a large nucleus, but there is no contractile vacuole. The anterior end of *N. magna* is embedded in an epithelial cell of the host to which it adheres by root-like processes (Fig. 4.2). The anterior end of *M. agilis* and *M. lumbrici* has a bluntly-pointed knob, the mucron.

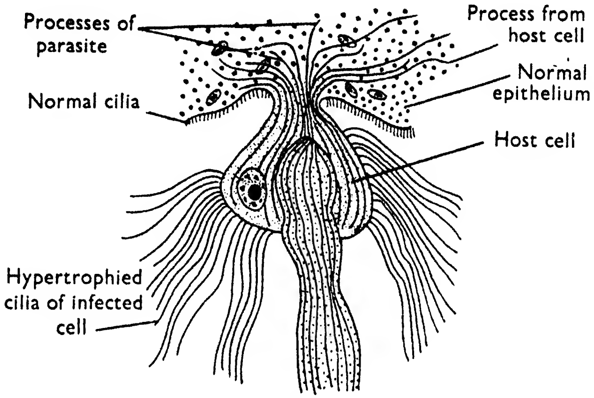


FIG. 4.2.—Anterior end of *Nematocystis magna* embedded in a cell of the host (after Hesse).—Redrawn from Mackinnon and Hawes, *An Introduction to the Study of the Protozoa*, 1961. Clarendon Press, Oxford.

REPRODUCTION

In the stage which we have just described, the animals are known as trophozoites. When they are full grown, two of them come together and form themselves into a rounded mass without fusing. Around this mass a two-walled cyst is secreted (Fig. 4.3). Each individual now divides by multiple fission, and gives rise to a number of small germ cells, a certain amount of residual protoplasm being left. The gametes unite in pairs, in which one member is probably derived from each parent.

Since all infections are mixed and culture has never been

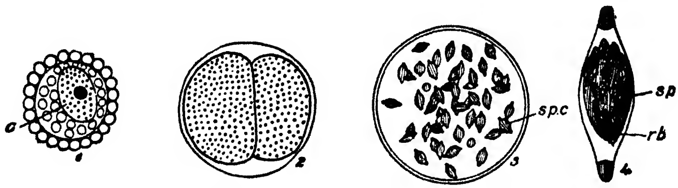


FIG. 4.3.—The life-history of *Monocystis*.—After Bütschli.

1. Young individual (*c*) lying within a sperm mother cell of an earthworm.
2. Association of two individuals within a cyst, ready to form gametes.
3. Numerous spore-cases (*sp.c.*, pseudonavicellæ) within a cyst.
4. A spore-case with eight spores (*sp.*) and a residual core (*rb.*).

achieved, it is not possible to assign particular types of cyst to particular species of trophozoite. It has been claimed that sometimes the associating pair are of different size and produce different types of gamete, so that they may be male and female, but more often no distinction can be made (Fig. 4.4). Each zygote is known as a sporont; it now secretes a boat-shaped, horny case known as a sporocyst.[1] Within the case the sporont divides by repeated fission into eight sickle-shaped sporozoites. There are thus two generations of spores in the life-history of *Monocystis*.[2] The cysts fall into the cavity of the body (the cœlom, see p. 158) and accumulate in the hinder segments, but no further development takes place until the sporocysts get free from the worm. This, presumably, sometimes occurs through the last few segments being broken off by autotomy (the fracture of a body or limb by its own contractions), or the parasite may have to await the death of the worm. In either case the cysts might later be swallowed by another worm with the earth from which it obtains its food, but proof of this is lacking. The sporozoites come out through a pore in the case and presumably bore their way through the wall of the gut and other tissues till they reach the vesiculæ seminales. Possibly, occasionally, the sporozoites pass directly from one worm to another during coition, but as young worms are free from parasites this is unlikely. In the vesiculæ seminales each sporozoite of *M. agilis* enters a sperm-mother-cell, where it grows by absorbing the protoplasm which is meant to serve for the nourishment of the spermatozoa (see p. 173). The latter are formed, but wither, their tails only remaining attached to the young *Monocystis*, which looks as though it had a coat of cilia. Finally they disappear, while the *Monocystis* continues to grow. Thus the sporozoites become trophozoites by development.

It has recently been claimed that some species of *Monocystis* ingest cells of their hosts and form food vacuoles as do other Protozoa. If this observation is confirmed they would be less modified for a parasitic mode of life than at first appears.

[1] It was formerly called a pseudonavicella, because of its resemblance to the diatom (a small plant) called *Navicella*; this word means a little boat, and refers to the shape of the organism.

[2] A spore is a small reproductive body formed by multiple or repeated fission. It may or may not be a gamete. If it be enclosed in a case it is known as a *chlamydospore* (e.g. pseudonavicellæ), if it be naked, as a *gymnospore* (e.g. those reported in *Amœba*). Amœboid spores are known as amœbulæ or pseudopodiospores, flagellate spores as flagellulæ or flagellispores.

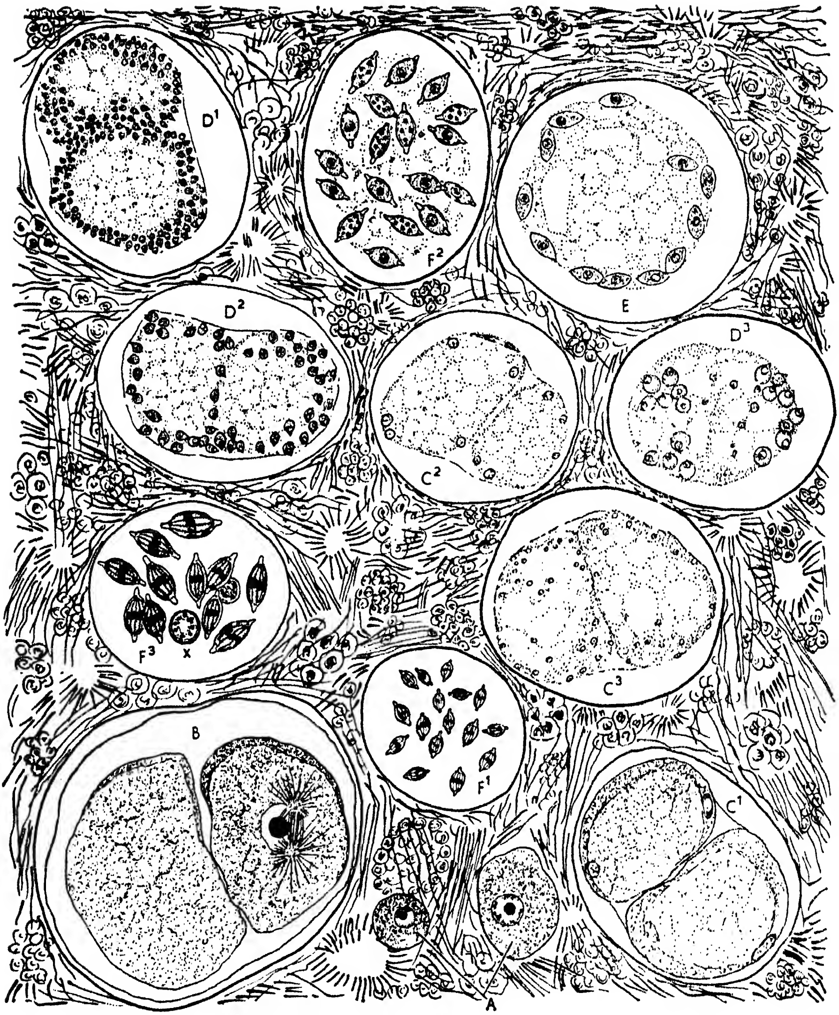


FIG. 4.4.—Monocystidæ. Composite drawing of several sections through heavily infected seminal vesicles of an earthworm. Stages in sporogony are set against a background diagrammatically representing spermatogenesis of the host. Dimensions of gametes and spores indicate the presence of at least 3 species of monocystids. Fixed B ; stained H. H. × 500 (Original D. L. M.).

A, trophozoites ; B–F, sections through gametocysts. B, gametocytes in gametocysts ; note endo- and ectocyst ; C^1–C^3, nuclei divide and become superficial ; D^1–D^3, gametes at surface of cytoplasmic residuum, which may contain a few degenerating nuclei : note 3 sizes of gametes ; E, zygotes ; F^1–F^3, sporogony (x in F^3, marks an equatorial section through a sporocyst, showing 8 sporozoites) : note 3 sizes of spores.—From Mackinnon and Hawes, *An Introduction to the Study of the Protozoa*, 1961. Clarendon Press, Oxford.

5

CILIATE PROTOZOA

PARAMECIUM

PARAMECIUM CAUDATUM, the slipper animalcule (Fig. 5.1), is a minute animal found in water in which dead leaves or other remains of organisms are decaying. The decay is brought about by bacteria, and upon these the slipper animalcules feed. A rich culture of *Paramecium* may be obtained by steeping hay in water, allowing it to decay, and adding to the infusion thus

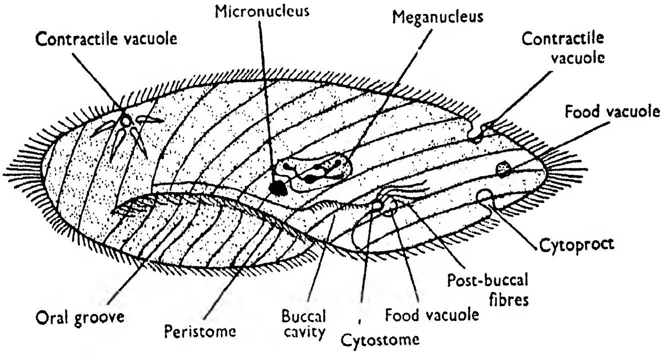


FIG. 5.1.—*Paramecium caudatum*. × 300.

made mud or weeds from a freshwater pond which contains *Paramecium*. The animals may easily be seen with the naked eye as minute, greyish white, oblong creatures, moving slowly about in the water. The body of *Paramecium* is spindle-shaped, somewhat flattened on one side, and with one end blunter than the other. The flat side is called ' ventral ' and the blunt end is anterior. This end appears as though it had been twisted, so that a groove which it bears is spiral, starting in front on the left and curving round to the ventral side, where it is continued back in the middle line to within about a third of the length of the body from its hinder end. From the groove there passes backwards into the body a funnel-shaped vestibule, the opening from vestibule

to endoplasm being known as the cytostome.[1] The whole body is covered with fine protoplasmic threads of the kind known as cilia (Fig. 5.2) by whose lashing the animal swims and gathers its food. The cilia are set at equal distances in rows, which run lengthwise in the hinder part of the body, but follow the spiral twist in front : they also line the vestibule, in whose inner part they form a complicated pattern leaving some areas bare. The

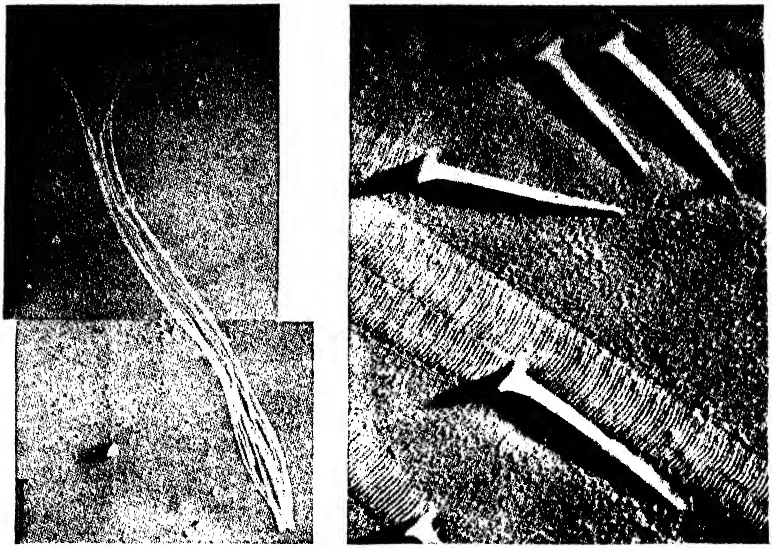


FIG. 5.2.—Electron photomicrographs of a cilium (on the left) and tips of discharged trichocysts of *Paramecium*. The cilium can be seen to consist of 11 separate threads. The measure in each photograph is 1 micron.—From Jakus and Hall.

cilia work regularly in waves, lashing backwards and driving the blunt end of the animal forwards with a left-hand rotating movement like that of a rifle bullet. A cilium has the same internal structure and the same type of basal body as a flagellum, and indeed it is difficult to distinguish the two in any formal way. Flagella are few and long, cilia are many and short.

ECTOPLASM AND ENDOPLASM

Paramecium has a soft, granular endoplasm and an ectoplasm which is firm and gives the body its shape, but elastic, so that the

[1] The nomenclature of the parts of a ciliate used in feeding has been confused. That used here is a simplification of the system proposed by Corliss, which in its full form does unnecessary violence to the English language.

animal can bend and squeeze through narrow gaps. The outermost layer of the ectoplasm is a tough pellicle. Below the pellicle comes the cortex, a thicker, clear layer of ectoplasm in which are embedded peculiar structures known as trichocysts (Fig. 5.2). These are spindle-shaped bodies with a fine point, placed at right angles to the surface, with the point in the outer part of the layer. If the animal be stimulated by impact or by a solution of some irritating substance, they suddenly elongate to about ten

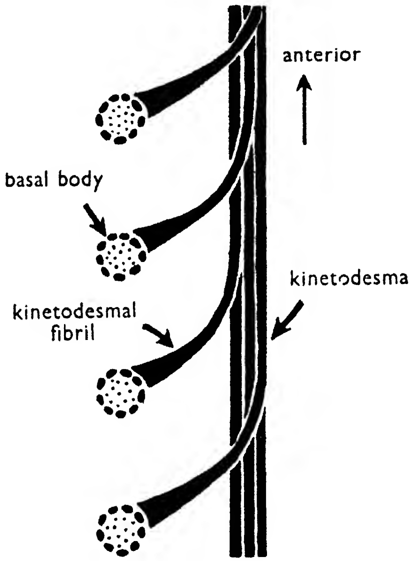


FIG. 5.3.—A diagram of a ciliate kinetodesma.—From Grimstone, *Biol. Rev.*, 1961, 36, 97.

times their resting length and project from the body as threads, of which the points, which in cross-section show much the same appearance as cilia, are sticky while the rest has hardened. The trichocysts are organs of adhesion by which the animal anchors. When it breaks free the threads are lost and the trichocysts replenished. The pellicle is marked by rows of hexagonal pits, in each of which a cilium arises, or sometimes a pair, while the trichocysts lie under the transverse ridges between the pits. From the basal body of each cilium runs a fibril, which joins with the fibrils from other cilia in the same row to make a kinetodesma, lying below and to the right of each longitudinal row of cilia

(Fig. 5.3). The fibrils taper and do not run the whole length of the kinetodesma. The endoplasm contains numerous granules, some of which appear to consist of waste matter ready for excretion, while others may be stored nutriment. Glycogen is diffused through the endoplasm.

NUCLEI

Paramecium caudatum has two nuclei, one of which is large and is known as the meganucleus, while the other, the micronucleus, is small and is situated in a groove on the meganucleus. The nuclei lie in the endoplasm above the cytostome ; *Paramecium aurelia* has two micronuclei.

There are two contractile vacuoles, which lie in the cortex of the dorsal side, one towards each end. At its full size each is a large spherical space surrounded by from six to ten pear-shaped radiating canals, whose wide ends lie under it (Fig. 5.4). These are the formative vacuoles. Systole affects only the central vacuole. After it has taken place, the formative vacuoles flow together at their inner ends and thus form the beginning of a new contractile vacuole, round which new canals appear, starting as mere slits and swelling to a pear shape by the enlargement of their inner ends. Over each contractile vacuole there is a minute gap in the pellicle, through which the contents of the vacuole are discharged.

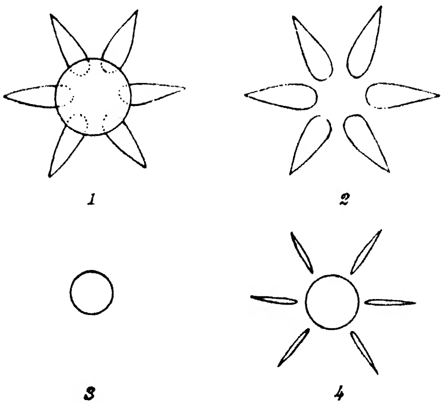


FIG. 5.4.—Successive stages of the contractile vacuole of *Paramecium*.

NUTRITION

The food consists of bacteria and other minute organisms. These are drawn towards the vestibule by the current set up by the cilia of the groove and driven down it to the cytostome by the specialised cilia. Particles appear to be forcibly sucked into the endoplasm so that a food vacuole is formed. It is carried by a streaming of the endoplasm around the body, passing

first backward along the ventral side, then forward nearly to the middle of the body, then through several turns of a short circuit in this region of the body, and finally forward to the front end and back so as to complete the circuit of the body (Fig. 5.5). During these wanderings the food is digested. The undigested remains are then expelled at a spot just behind the cytostome, where a passage through the ectoplasm, known as the cytoproct, is formed when it is required. As in *Amœba*, digestion takes place in an acid vacuole and protein is the chief food. The formation of the vacuoles and their acidity are easily demonstrated if a suspension of 1 g. of yeast and 10 mg. of Congo Red is boiled for ten minutes with a few millilitres of water and then fed to the ciliates. The indicator turns blue at pH 3. The animal is able to some extent to distinguish between particles which are good for food, and those such as carmine which are inert. Moreover, having been deceived experimentally by carmine it learns to avoid it in the future, and can remember to do so for two or three days.

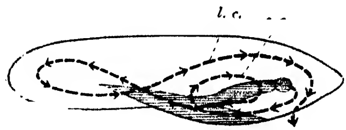


FIG. 5.5.—A diagram of the course of the circulation of the food vacuoles in *Paramecium*.
l.c., Long circuit ; *s.c.*, short circuit.

EFFECT OF STIMULI

Like all other organisms, *Paramecium* shows automatism. Its incessant activity is spontaneous, but is continually modified by external stimuli. The movements of *Paramecium* are much more active and definite than those of *Amœba*, and it is correspondingly easier to observe the effect of various stimuli upon the animal. These effects are of two kinds, of which the first is merely an alteration in rate of movement. Many acids, alkalis, salts, and other substances in dilute solutions cause an increase in the rate of motion owing to a more rapid working of the cilia. Increase of temperature up to about 35° C. has the same effect. On the other hand, dilute solutions of narcotics, such as alcohol, ether, or chloroform, cause the cilia to work more slowly. All these reactions may be merely the products of the direct effects which such changes in the environment are known to have upon protoplasm. Many of the above also have another effect, although this may only be produced at a critical point. They cause the animal to give a particular response known as the avoiding reaction

or phobotaxis ; the creature stops, may swim a short distance backwards, and then moves forwards again at an angle to its previous path. By these means it can avoid a solid obstacle, hot water, or an acid, and if it is placed in a situation where there is a continuous gradient, e.g. of temperature, it may appear to be attracted, for example, to the cool end ; in reality, as can easily be seen with a low-powered microscope, it is repelled from the hot, (Figs. 5.6, 5.7). In the same way it may become trapped in a drop of acid. *Paramecium* has two other types of response ; under some circumstances contact with a solid body, especially on two sides at once, as when it swims into a corner, causes protrusion of the trichocysts, and this can also be induced by chemicals such

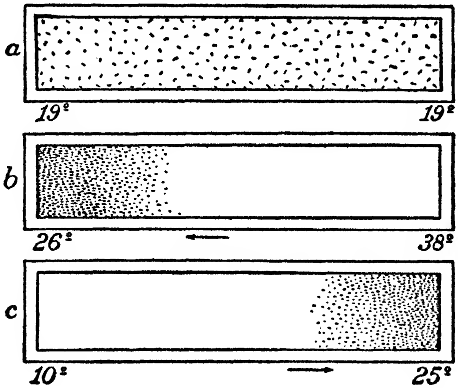


FIG. 5.6.—The reaction of *Paramecia* to heat and cold.—From Jennings, after Mendelssohn.

At *a*, the *Paramecia* are placed in a trough both ends of which have a temperature of 19° C. They are equally scattered. At *b*, the temperature of one end of the trough is raised to 38° C., while the other is only 26° C. The *Paramecia* collect at the end which has the lower temperature. At *c*, one end has a temperature of 25° C., while the other is lowered to 10° C. The animalcules now collect at the end which has the higher temperature.

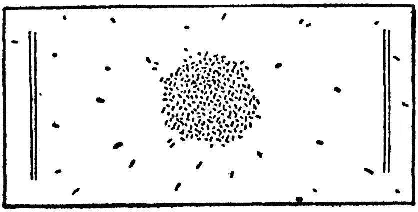


FIG 5.7.—*Paramecia* collecting in a drop of 0·02 per cent. acetic acid.—From Jennings

as tannic acid; lastly, when two *Paramecia* meet they may adhere in conjugation (see below). These two responses suppress the avoiding reaction which is normally produced by the stimulus of contact.

REPRODUCTION

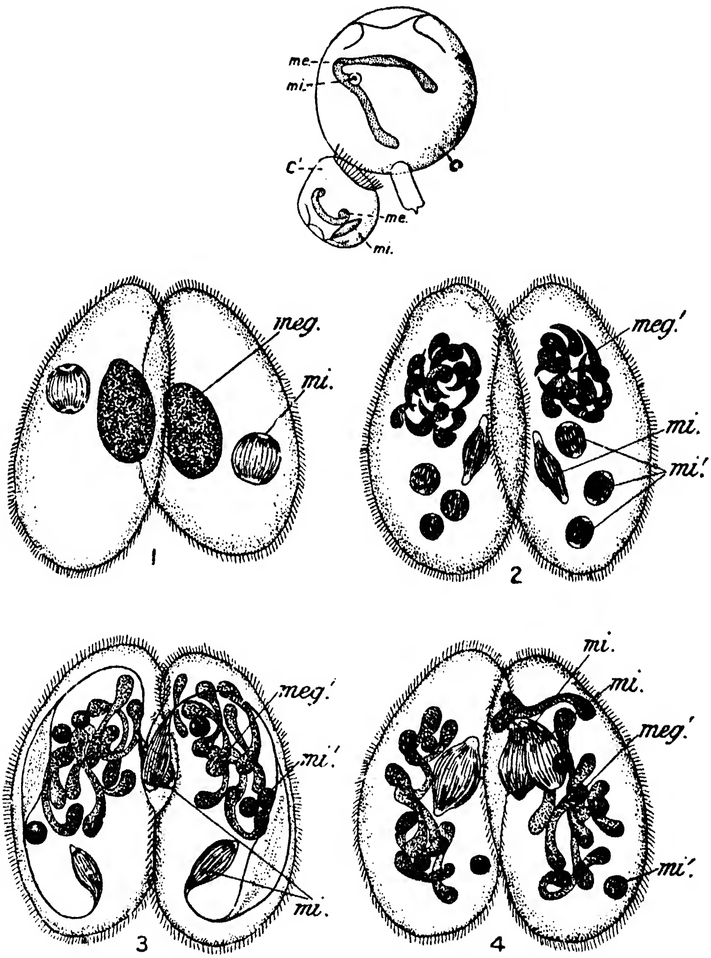
Paramecium reproduces by binary transverse fission. The meganucleus divides amitotically, that is, without division of the constituent chromosomes (p. 702) or separation of their pairs, the micronucleus by a mitosis in which, as in that of *Amœba*, the nuclear membrane does not break up, and the place of centrosomes is taken by pole plates. Meanwhile a groove appears round the middle of the body and deepens till the cytoplasm is split into two, each half containing a daughter nucleus of each kind and one of the contractile vacuoles, while only the anterior half possesses a mouth. Development involves not only growth but also the remodelling of the body, since each half lacks some of the outward organs of the parent, while those which it has are too large for it. The new cytostome of the posterior daughter arises from a non-ciliated region. In a well-fed culture, division takes place two or three times a day, but if the animals be ill-nourished it is much less frequent, and if they be starved they cease to divide.

CONJUGATION

The conjugation of *Paramecium* is a remarkable process, of a kind found only in this creature and in the other members of its class (Figs. 5.8, 5.9). As a rule, the process begins during the late hours of the night and lasts till the next afternoon. The details differ in different species, but the following is the usual course of events in *P. caudatum*. Two individuals, which we will call conjugants, come together as those of *Monocystis* do, but without encysting, and lie with their ventral sides touching, the endoplasms becoming continuous in the region of the gullets, which degenerate. The micronucleus of each conjugant leaves its normal position, lies free in the cytoplasm, and grows larger. It then divides twice, and three of its four products degenerate. The remaining micronucleus divides again, this time somewhat unequally, the smaller product being the male nucleus, the larger

the female nucleus. At this stage we may regard each conjugant as containing two gametes, the male, represented only by its nucleus, the female by the nucleus plus the cytoplasm of the

A



B

FIG. 5.8.—Conjugation in Ciliata.

A, *Vorticella* ; *B*, *Paramecium*.

c, Pseudo-female conjugant ; *c′*, pseudo-male ; *me.*, *meg.*, meganuclei ; *meg′.*, disintegrating fragments of meganucleus ; *mi.*, micronuclei; *mi′.*, abortive micronuclei.

conjugant. These are analogous to a spermatozoon and an ovum, so that the animal may be said to be hermaphrodite. The true syngamy now takes place The male pronucleus of each conjugant. passes over into the other and fuses with the female pronucleus of

the latter and there is also some mixture of cytoplasm. The body which belonged to each conjugant comes thus to contain a micronucleus of mixed origin. It is, in fact, a zygote. The zygotes separate and are known as exconjugants. During conjugation the meganucleus degenerates, splitting up into shreds, which disappear. After separation the zygote nucleus of the exconjugant undergoes a development whereby nuclei of both kinds are provided. It divides three times successively, so that the body contains eight nuclei. After an interval the body divides into two, each half containing four nuclei, and after a further interval these halves divide, so that there are four individuals, each with two nuclei, one of which becones a meganucleus and the other a micronucleus. Breeding experiments suggest that meiosis (p. 700) takes place either in the first or in the second division of the micronucleus of the conjugant.

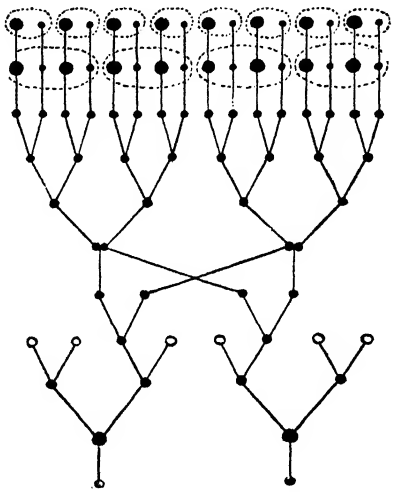


FIG. 5.9.—A diagram of the behaviour of the micronuclei of *Paramecium caudatum* during conjugation. The white circles represent the portions that degenerate.

The conditions under which conjugation takes place in *Paramecium* have been, and are still, the subject of much investigation. Many points still remain to be cleared up, but certain results have now been reached. Conjugation generally occurs at the beginning of a falling off in the supply of food after a period of exceptional plenty that has brought about rapid multiplication. Thus it will often take place in an infusion in which the bacteria, having used up the nourishment provided by the plant-remains, are falling off in numbers, and thus the animals, after a plentiful supply of food, are beginning to experience dearth. Each species of *Paramecium* can be divided into a number of varieties which will not conjugate with each other. Each variety is again divisible into two or sometimes more mating-types, each of which is self-sterile but will conjugate with all other types

within the variety. Varieties and mating-types have no known morphological distinctions. There are some races in which it is difficult to bring about conjugation, others in which it has never been seen, and yet others in which it takes place at short intervals without apparent cause. It seems that each clone, that is, the population derived by asexual reproduction from a single parent, has its own life-history. At first it is sexually immature, and this phase lasts in *P. bursaria* for several months. Then, for years there is sexual maturity, and conjugation readily takes place. Finally the stock seems to age, and may die out. The species is apparently maintained by occasional very vigorous products of conjugation. Many exconjugants die at once, or after a few divisions.

Paramecium also has a type of pseudo-sexual process known as cytogamy, which is similar to conjugation except that the fusing micronuclei come from the same parent, so that it is a form of self-fertilisation. In yet another variant much the same nuclear changes go on as in conjugation, but in a single individual. The meganucleus disappears, the micronucleus divides a number of times, and new individuals, with new nuclear outfits, are formed by fission. According to some workers that is all that happens and the process is endomixis, but the majority claim that the last surviving pair of micronuclei immediately fuse with each other, so that the process is autogamy, another form of self-fertilisation. Whichever it may be, it seems to have some of the same good effect on a culture as does conjugation.

Laboratory stocks of *Paramecium* often show a condition called depression. The meganucleus is enlarged and there are changes in the shape of the body, and death follows. Various changes in the environment can alleviate depression, and it is probable that the cause lies in unnatural conditions of culture.

Genetical experiments have shown that the characters of an individual paramecium are determined by its meganucleus, and this is in agreement with the fact that ciliates without micronuclei can generally carry out all functions except those of conjugation and endomixis, while loss of the meganucleus always leads to death within two days. It is obvious that *transmission* of hereditary characters can take place only through the micronucleus, since the other is destroyed.

VORTICELLA

Among the most beautiful forms of pond life are the bell-animalcules, many of which are of the genus *Vorticella* (Figs. 5.10, 5.11). Various species may be found as minute, colourless bodies fastened to weeds by stalks which contract at the slightest disturbance of the water. Some of them also appear in infusions. The body of a *Vorticella* is outwardly shaped like a bell, but has no hollow within, the bell being filled with a mass of protoplasm. In the place of the handle is a long stalk, by which the animal is fastened to some solid object. Animals which are thus fixed are said to be sessile. The bell can be bent upon the stalk. The wide end of the bell has a thickened rim, within which is a groove, the peristome. On one side there passes from the peristome, down into the mass that fills the bell, a tube which is the vestibule. The part of the upper surface which is encircled by the peristome is known as the disc. It is not level, but slopes, being raised on the side where the gullet lies. The disc can be retracted, and the rim of the peristome drawn inward over it. Around the edge of the disc and down into the vestibule three rows of cilia wind spirally counter-clockwise, the two inner long and upright, the outer short and slanting outwards. In the vestibule the members of the outer row beat together to form an apparent undulating membrane. There are no cilia elsewhere upon the body.

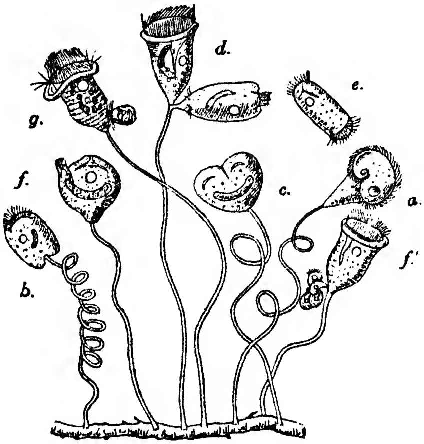


FIG. 5.10.—A group of individuals of *Vorticella* in various phases of the life-history.

a, Ordinary individual; *b*, the same contracted; *c*, ordinary fission; *d*, a later stage of the same; *e*, free swimming individual produced by ordinary fission; *f*, *f'*, two modes of fission to form a conjugant; *g*, conjugation.

ECTOPLASM AND ENDOPLASM

The general character of the ectoplasm and endoplasm is the same in *Vorticella* as in *Paramecium*, but the pellicle of the bell-animalcule is sculptured in various ways according to the species, and below it is a distinct alveolar layer so called because the protoplasm appears to be full of bubble-like spaces or alveoli. Just under the alveolar layer, in the walls of its bubbles, is a layer

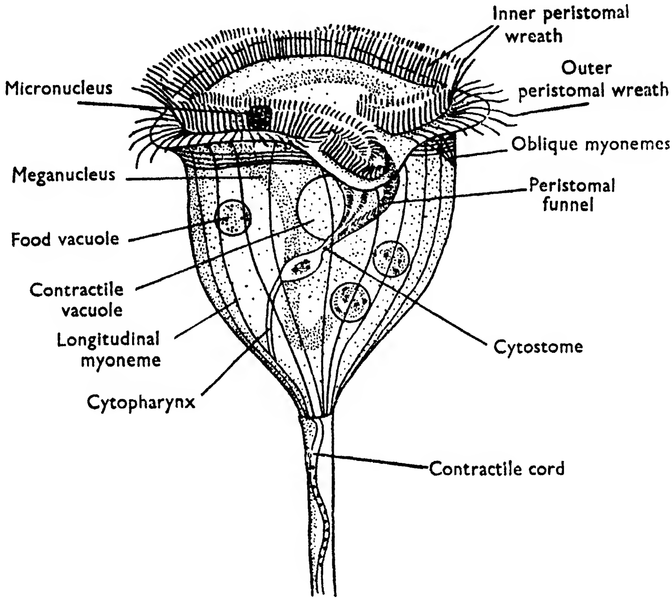


FIG. 5.11.—*Vorticella*, × 1,000.—Redrawn from Mackinnon and Hawes, *An Introduction to the Study of the Protozoa*, 1961. Clarendon Press, Oxford.

of very fine contractile fibres or myonemes. Near the stalk the ectoplasm is much thickened and the myonemes pass inwards through it to run down the stalk as a bundle of filaments, the spasmoneme. There are no trichocysts. The endoplasm is granular.

INTERNAL ORGANS

A meganucleus and a micronucleus are present, the former a long, curved band, the latter small and placed beside the meganucleus, usually in the upper part of the body. There is a contractile vacuole, which has no canals. It lies in the upper

region of the body and communicates with the vestibule through a reservoir, which has a narrow permanent opening. The contractile vacuole contracts sharply at intervals, discharging into the reservoir. The latter then contracts slowly, driving its contents into the vestibule, but not itself disappearing. Feeding and digestion take place much as in *Paramecium*. The little organisms which serve as food are collected and driven into the vestibule by the action of the cilia. The food vacuoles follow a definite, winding course in the body, passing through stages similar to those in *Paramecium*. The fæces are discharged into the vestibule by a pore, which in some species is a permanent cytoproct.

REPRODUCTION

The reproduction of *Vorticella* takes place by binary fission, which is of two kinds—ordinary fission, and that which forms conjugants. In ordinary fission, the rim closes in over the disc, the body becomes shorter and wider, and the meganucleus contracts and lies across the body, which then divides into two, the plane of fission being in line with the stalk. The nuclei behave as in *Paramecium*. One of the daughters remains upon the stalk ; the other grows a circlet of cilia in the aboral region (that is, away from the mouth), at the level at which the ectoplasm thickens ; this daughter then breaks off and swims away, aboral end in front, and settles elsewhere to grow a new stalk from its anterior end. In this form of reproduction the offspring are equal in bulk. In the fission which forms conjugants the parent gives rise to one large individual and one or more of a smaller size. The small individuals may arise by unequal binary fission, sometimes called budding, or by equal fission, followed by division of one product into four by repeated fission.[1] The small individuals, by whichever method they are formed, resemble the free product of ordinary fission in all but size.

CONJUGATION

The small individuals thus formed swim away, and since they do not feed cannot live for more than 24 hours. One may attach itself by the aboral end to the lower part of the body of a stalked

[1] The various kinds of fission of *Amœba*, *Vorticella*, and animals related to them (Protozoa, p. 76) may be classed as : (1) equal binary fission (p. 32), (2) budding, (3) repeated fission (p. 35), (4) multiple fission (p. 33).

conjugant. Most of the organs of the small individual now disappear, and the ectoplasm between the two is absorbed into their endoplasm, which becomes continuous. The meganucleus in each begins to break up and disappear. Meanwhile the micronucleus of the small conjugant has divided into two. Now the micronuclei of both conjugants divide twice, so that the larger contains four and the smaller eight micronuclei. In each conjugant all but one of these perish and the survivor divides into two, which correspond to the male and female nuclei of *Paramecium*. This division takes place while the two micronuclei are lying in the region where the endoplasm of the conjugants became continuous. One half of each micronucleus passes into the larger conjugant, where the two fuse as male and female nuclei. The other half of each passes into the smaller conjugant, but these halves, instead of fusing, degenerate and disappear. The endoplasm of the small exconjugant is now drawn into the larger, the ectoplasm shrivelling up and falling off. It will be seen that the conjugation of *Vorticella* takes place in the same way as that of *Paramecium*, but that one of the two exconjugants perishes and is partly absorbed by the other.[1]

OTHER STALKED CILIATES

Carchesium is a small freshwater animal whose body consists of a number of members, each of which has the structure of a whole *Vorticella*. It arises from a *Vorticella*-like body, by divisions like those which take place in the ordinary reproduction of *Vorticella*, save that the division passes some way down the stem and then stops, leaving the bells joined by their stalks. Thus the body is increased by the addition of new members which repeat the structure of the old. The whole body of a *Carchesium* is said to be a colony, and its members are zooids. Reproduction is brought about by the complete fission from the body of certain zooids, which thus become asexually produced young (buds). Each of these swims off, settles down, and forms by growth and nuclear division a new colonial individual. Conjugation like that of *Vorticella* also takes place. Each bell of *Carchesium* has its own spasmoneme, and contracts independently of its neighbours ;

[1] The student should beware of comparing the smaller conjugant of *Vorticella* with a spermatozoon and the larger with an ovum. Ova and spermatozoa are gametes of unlike kinds. The conjugants of *Vorticella* are unlike, hermaphrodite parents, each of which forms two unlike gametes.

Zoothamnium is much like *Carchesium*, but there is one continuous branched spasmoneme, and the whole colony contracts together. ***Epistylis*** is colonial but non-contractile. Many species of ***Epistylis*** and some of *Carchesium* are epizootic on freshwater Crustacea and other animals.

CILIATES OF THE FROG

The rectum of the frog contains an interesting population of ciliates, which live chiefly in the lighter-coloured contents of its

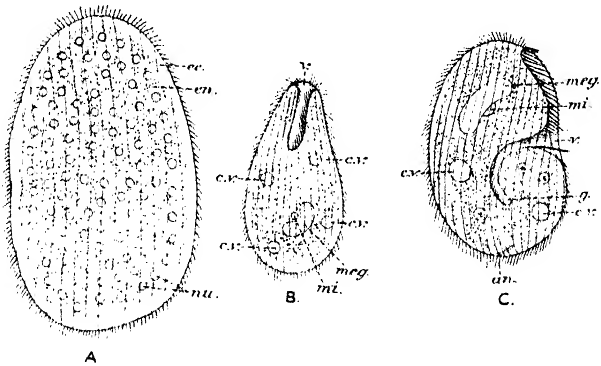


FIG. 5.12.—Ciliata from the rectum of the frog.

A, *Opalina ranarum* ; *B*, *Balantidium entozoon* ; *C*, *Nyctotherus cordiformis*. *an.*, Cytoproct ; *c.v.*, contractile vacuoles ; *ec.*, ectoplasm ; *en.*, endoplasm ; *g.*, vestibule ; *meg.*, meganucleus ; *mi.*, micronucleus ; *nu.*, nuclei ; *v.*, peristome.

foremost region (Figs. 5.12, 5.13). *Balantidium entozoon* differs from *B. coli* (p. 75) in having four contractile vacuoles and a longer peristome. *Nyctotherus cordiformis* resembles the *Balantidia* in its general features, but is bean-shaped, with a long vestibule placed in the middle of the hollow side and bearing a wreath of long cilia, one contractile vacuole in the hinder part of the body, and a permanent cytoproct, lined with ectoplasm, at the hind end.

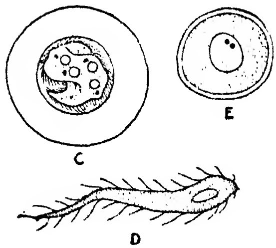


FIG. 5.13.—*Opalina ranarum*.

C, small encysted individual (distributive phase); *D*, gamete; *E*, encysted zygote.

More numerous and conspicuous than either of these is *Opalina ranarum*, a flat, oval, pale-straw-coloured ciliate of very large size (1 mm. long), uniformly covered with equal cilia, and without

mouth, peristome, contractile vacuole, or trichocysts. It has many nuclei, unlike those of other ciliates in being all of one kind. The life-history is also very unlike that of other ciliates. Nuclei and cytoplasm divide independently and during the greater part of the year keep pace with one another and with growth, so that the appearance of the mature animals remains the same ; but in the spring the division of the cytoplasm gains, so that small individuals with 3-6 nuclei result. The little individuals now encyst. The cysts are passed by the frog into the water and there swallowed by tadpoles, in which they hatch, and their cytoplasm divides to form uninuclear gametes, the nuclei meanwhile probably undergoing a reducing division. The gametes conjugate, and the zygote encysts. Probably it always at this stage passes out of the host and enters another, where it hatches. From the cyst emerges a uninuclear ciliate which grows into the adult. During the whole process cilia are lost only in the zygote cyst.

6

THE PROTOZOA AS PARASITES OF MAN

The interest which the study of the Protozoa has for mankind is not merely theoretical, in virtue of the remarkable peculiarities of their organisation, but is very near and practical, by reason of the fact that a number of them live in the bodies of man,

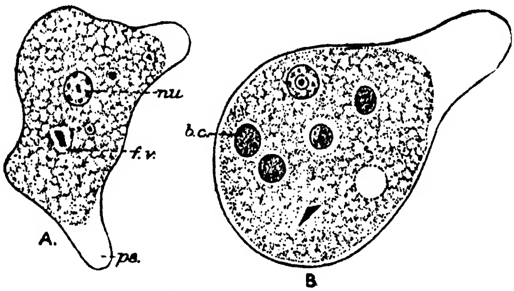


FIG. 6.1.—*Entamœba.* × *c.* 1,000.—After Fantham.
A, *E. coli*; B, *E. histolytica.*
b.c., Ingested red blood corpuscle; *f.v.*, food vacuole; *nu.*, nucleus; *ps.*, pseudopodium.

and that there they sometimes cause serious diseases. In this chapter we shall study briefly examples, drawn from all the four classes of the group, of which man is a host—that is, which he harbours as parasites.

ENTAMŒBA

Two species of *Entamœba* (Fig. 6.1), a genus with one or two large blunt pseudopodia, chiefly composed of ectoplasm, and no contractile vacuole, live in the hind gut of man. *E. coli* is about 20–35 μ in diameter, and lives in the upper part of the large intestine, feeding upon the bacteria which infest that region, and also upon the remains of the food of its host. It never attacks the tissues of its host and is harmless, and possibly sometimes even beneficial by keeping down the bacteria. In the intestine it reproduces by binary fission, and some of the small products of fission beome rounded and encyst. In the cyst there is at first

a single nucleus, but this divides to form eight. The ordinary *Entamœbæ* die in the fæces. So do the cysts if the fæces dry,

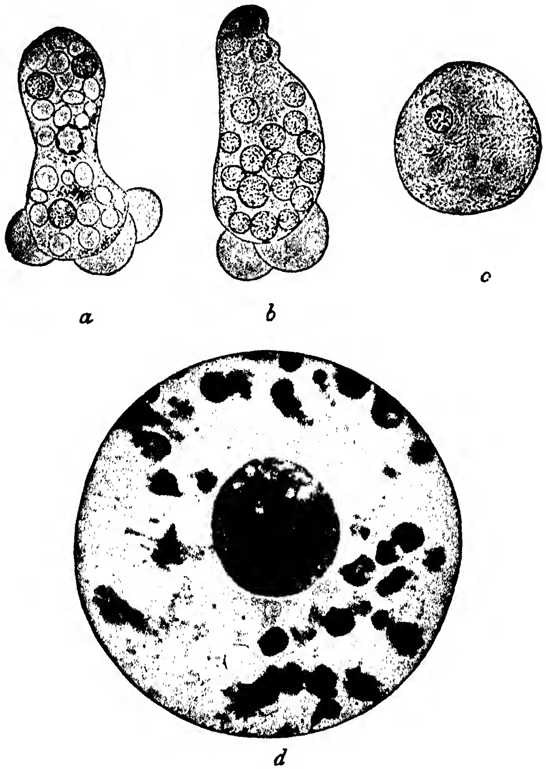


FIG. 6.2.—*Entamœba histolytica.*

a and *b*, Amœbæ as seen in fresh stools, showing blunt ectoplasmic pseudopodia, non-contractile vacuoles, ingested red corpuscles, and, in *a*, nucleus; *c*, an amœba as seen in a fixed preparation; *d*, section of wall of liver abscess, showing an amœba of spherical form. The rounded amœbæ on this plate must not be confused with the encysted form.

but if they remain moist until they reach water or human food and are swallowed by a man the cysts germinate in the intestine of the new host; the protoplasm escapes from the cyst as a syncytium with eight nuclei, but the cytoplasm divides so that eight small amœbæ are formed. By these the cycle is re-started.

Entamœba histolytica also inhabits the human large intestine (Figs. 6.2, 6.3). It has about the same range of size as *E. coli*,

from which it differs in being more active, in having a distinct ectoplasm over the whole surface of the body, in taking up strongly, while still alive, the stain known as 'neutral red', and in that the principal chromatic body or 'karyosome' of the nucleus is centrally placed. Unlike *E. coli* it may attack the mucous membrane of the intestine, probably by the secretion of an enzyme, so forming ulcers. Some individuals penetrate the blood vessels in the same way, and are carried by the circulation to the liver, where they may set up abscesses. When living free in the gut it feeds on fæcal particles just as *E. coli* does, but when it invades the tissues its chief food is red blood cells; it can also absorb liquid food. *E. histolytica* is found all over the world, but only about ten per

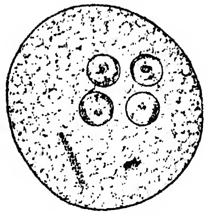


FIG 6 3—*Entamœba histolytica* in the encysted condition—After Fantham.

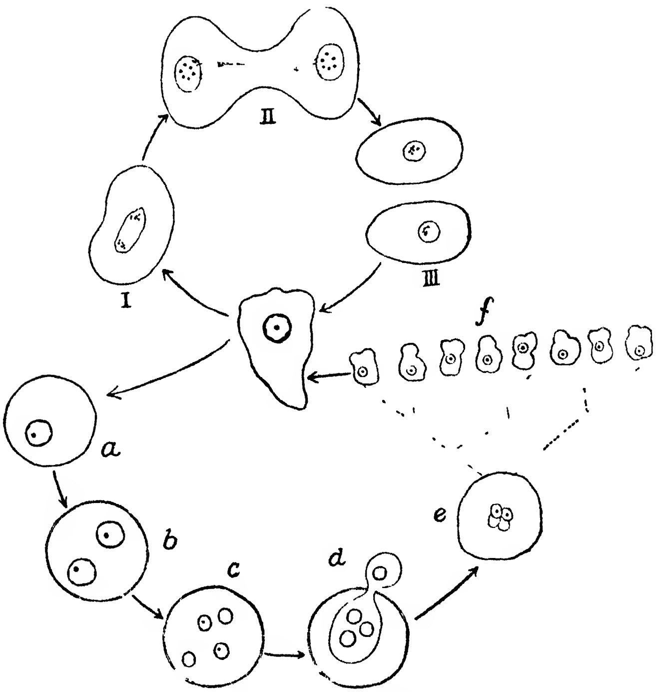


FIG. 6.4.—The life-cycle of *Entamœba histolytica*.

I–III, Binary fission; *a–f*, encystment and multiple fission.
4. Rounding off; *b*, cyst in which the nucleus has divided; *c*, cyst in which the second division has taken place; *d*, emergence from the cyst; *e*, free amœboid individual with four nuclei which lie close together; *f*, eight amœbulæ formed from *e* by a complicated process of division.

cent. of those human beings who are infected show clinical symptoms of its presence in the form of dysentery. Its life-cycle (Fig. 6.4) appears to differ from that of *E. coli* chiefly in the number of the cyst nuclei, of which there are only four, though after emergence these divide with the cytoplasm to form eight little amœbæ. The cysts are the only infective forms, and are acquired through food or water often from carriers who do not show the disease.

TRYPANOSOMA

Flagellate Protozoa of the genus *Trypanosoma* are responsible for various very dangerous diseases of man and animals in warm countries. They are parasitic in the blood and other fluids of backboned animals, but at one stage in the life-history live in invertebrates which suck the blood of the vertebrate hosts. The body (Figs. 6.5, 6.6) is a ribbon of protoplasm about one-thousandth of an inch in length, tapering towards the ends, but more pointed in front than behind. The shape of the body is maintained by a strong pellicle. A single flagellum stands at the front end, and from its base an undulating membrane runs along one side nearly to the hind end ; the undulating membrane of related flagellates has been shown to be formed partly from the cell membrane and partly from the greatly expanded membrane of the flagellum (Fig. 7.1). The flagellum is continued as a strongly-staining thread along the free edge of the membrane, and terminates behind a minute basal body, embedded in the cytoplasm. By the working of the undulating membrane and flagellum the animal swims rapidly with a graceful wavy movement, either forwards or backwards. There is no contractile vacuole. Near the middle of the body is an egg-shaped nucleus, and a smaller mass, which stains like the nucleus, is in contact with the basal body. It is known as the kinetoplast, but though it contains deoxyribonucleic acid, its functions are unknown. *Trypanosoma* has no mouth, but nourishes itself, like *Monocystis*, by absorbing through the surface of its body substances obtained from the juices of its host. Strains of trypanosomes without kinetoplasts occur naturally, and can also be induced experimentally.

The only known method of reproduction is by longitudinal binary fission, in which the basal body divides, one anterior

half going with the old flagellum to one daughter, one posterior growing a new flagellum for the other.

In spite of the immense amount of investigation of which its medical importance has caused it to be the subject, the life-history of *Trypanosoma* is not yet thoroughly understood. In

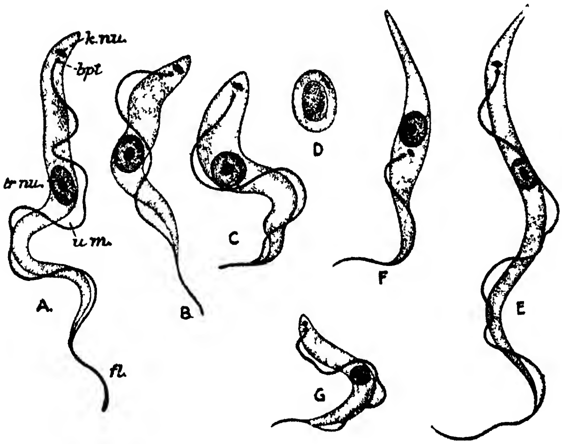


FIG. 65. *Trypanosoma gambiense*

A, *B*, *C*, Slender, intermediate, and stumpy forms from man. *D*, 'latent body'. *E*, slender form from gut of fly. *F*, crithidial form from salivary gland of fly. *G*, ripe form from proboscis of fly.
bpt, basal body; *fl*, flagellum; *k. nu*, kinetoplast; *tr. nu*, nucleus; *u. m*, undulating membranes.

the case of *T. gambiense*, the cause of the terrible sleeping sickness of West and Central Africa, the following facts have been established. In the body of an infected man the parasites live at first in the blood, but presently make their way into the lymphatic glands, and thence into the fluid of the spinal canal and cavities of the brain. While they are in the blood alone the man suffers from 'Gambia fever', but when they reach the central nervous system the drowsiness which is characteristic of sleeping sickness comes on, and increases, and is followed by a wasting of the body, till death almost inevitably results. The individuals found in the human host are not all alike, some being long and slender, some short and stumpy, and some intermediate in shape. The thin forms are the youngest, the animals growing stouter as they mature, and becoming stumpy in succeeding generations. There are also differences in size, due to age and to the fact that the fission is sometimes unequal.

During the progress of the infection some of the trypanosomes pass into certain of the internal organs of their host, especially into the spleen and lungs. There they lose their flagella and become an oval shape. In this condition they show resemblances to the predominant phase of the organism known as *Leishmania*, which is the cause of the kala-azar disease and of Delhi boil.

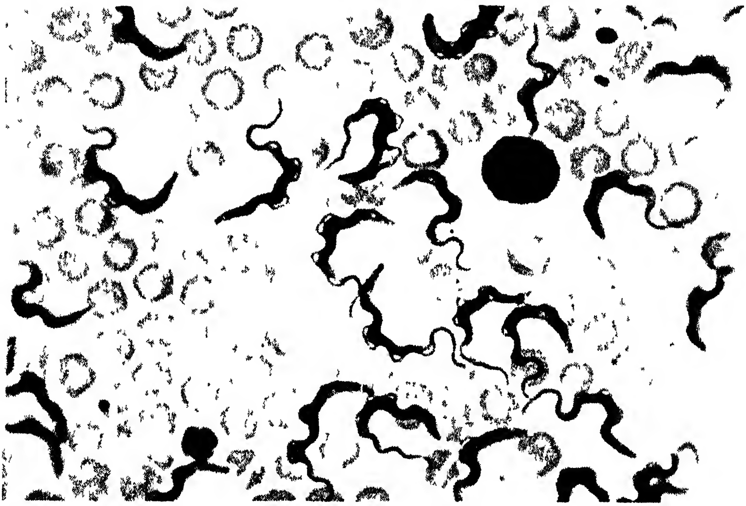


FIG. 6.6—*Trypanosoma cruzi*. Experimental infection in mouse blood, showing red blood cells and parasites × c. 900.—Photograph by Prof. J.F.D. Shrewsbury

True *Leishmania* stages, which presently revert to the flagellate condition, do occur in the life-cycles of other trypanosomes. It has been supposed that these phases of *T. gambiense* are of a similar nature and that they revert and thus make good the loss of flagellates in the blood when, as happens between the fits of the fever, the flagellates are reduced in number by the secretion of 'antibodies' (p. 149) by the host. On this theory they have been called 'latent bodies'. It is more probable, however, that they are individuals in a state of degeneration.

The invertebrates responsible for the spreading of *Trypanosoma gambiense* are the tsetse flies, *Glossina palpalis* and *G. tachinoides* (Fig. 6.7). These are similar in size and general habits to the clegs of the English countryside. They suck the blood of various backboned animals—cattle, antelopes, birds, reptiles, and so

forth, as well as man—and thus take into their stomachs such parasites as may infest the blood vessels of its victims. When the object of the attack of *Glossina* is infected with the trypanosome of sleeping sickness, the insect becomes capable of inoculating a new host in the course of its feeding. The power is soon lost, but is regained after about twenty days. It seems probable that the first inoculations are made with trypanosomes which are still fresh in the proboscis of the insect, but the later ones with individuals which arise from the stumpy forms after passing through a course of development in the insect's alimentary

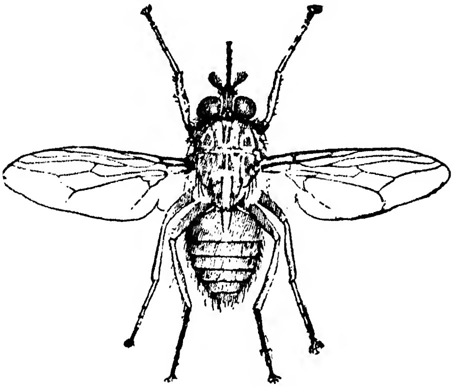


FIG. 6.7.—The tsetse fly *Glossina palpalis*.—From Thomson.

canal and salivary glands. During this development the stumpy forms become first long and slender, then, attached to the wall of the salivary gland, they pass through a 'crithidial phase' in which the membrane starts in front of the nucleus; finally, as stout-bodied, mature individuals, they are injected with the saliva when a new victim is bitten.

Besides *T. gambiense* there are known a number of other trypanosomes: *T. rhodesiense* which causes a sleeping sickeness in the southern part of Central Africa, and is transmitted by *G. morsitans*, *G. swynnertoni* and *G. pallidipes*; *T. brucei*, the cause of a disease of horses and cattle in South Africa; *T. equinum* which causes a horse disease in South America; *T. cruzi*, the cause of a disease in children in the same continent, and so forth. The same species has sometimes been described from different parts of the world and given more than one name, so that there is much confusion. Not all trypanosomes are carried by tsetse flies. Many, perhaps all,

have a wild host in which they are harmless, though in the unaccustomed bodies of men or domestic animals they are highly dangerous. Formerly no treatment was of any avail against them; recent research has produced several synthetic drugs, mainly organic compounds of arsenic and antimony, which can cope with at least the African species, but the best way to combat them is to avoid the attacks of the insects which transmit them. Thus the clearing around places frequented by human beings of the bush which is the haunt of *Glossina* has led to a decrease in the number of cases of sleeping sickness.

PLASMODIUM

MALARIA PARASITES

The disease malaria or ague is a fever found in almost all parts of the world, but in its most severe forms characteristic of warm regions. Where it is endemic it has been responsible for public lassitude and a low standard of living, and when it has affected invading armies, from those of Alexander to Allenby, it has influenced the fate of nations in another way. It is caused by parasites of the genus *Plasmodium*,[1] belonging, like *Monocystis*, to the Sporozoa. Four species occur in man: *P. vivax*, *P. ovale*, *P. malariæ*, and *P. falciparum*. All have complicated life-histories; those of the first two are alike except in details, that of *malariæ* is probably similar, and that of *falciparum* differs in one important respect.

It is convenient to begin the cycle at the point when a man is bitten by a gnat (or mosquito, for those who prefer the Spanish name for the same insect) already infected by the parasite. When the gnat has pierced the skin (p. 239), and before it begins sucking blood, it injects a small quantity of saliva containing an anti-coagulant, and in this are present small stages of the parasite known as sporozoites. Within about half an hour afterwards all of these have disappeared from the blood, and within a few days parasites can be found inside cells of the man's liver. At first very small, they grow rapidly, so that they almost fill the host

[1] It is unfortunate that this word is also used to denote a type of relation of nuclei to cytoplasm—that in which a syncytium is formed by the fusion of free cells (p. 409)—which, as it happens, is not found in the malarial parasite.

cell, pushing its nucleus to one side. At the same time the nucleus of the parasite has divided repeatedly, so that when this stage, the schizont, is fully grown, some thousands of nuclei are present. Eventually the host cell bursts, and the cytoplasm of the sporont falls apart into schizozoites, each with one nucleus.

This part of the cycle, called pre-erythrocytic, takes from five to nine days, depending on the species and perhaps on the strain of the parasite. At the end of it the liberated schizozoites enter the blood, and begin the second, or erythrocytic, part of the life-history, by penetrating the red blood cells or erythrocytes. Only one schizozoite enters each cell, and it then grows to form a trophozoite. This at first is rounded, with one nucleus, and contains a large vacuole, which makes it look like a ring (Figs. 6.8 and 6.9). In other species of *Plasmodium*, and presumably in those of man, the vacuole is formed by a process similar to pinacytosis (p. 27), and in it the hæmoglobin of the host is broken down. The parasite grows, loses its ring-like appearance, and develops pigment, and at this stage *P. vivax* becomes amœboid. When it is mature it is once again a schizont ; the pseudopodia are withdrawn, the nucleus divides repeatedly to form 16, and cytoplasm collects round each of these to form schizozoites, leaving some cytoplasm in the middle of the cell. The wall of the red cell bursts, setting free the schizozoites, each of which penetrates a new red cell to start a fresh cycle.

The crisis of the fever is caused by the almost simultaneous bursting of the red cells, probably because of the waste products that are liberated at the same time as the schizozoites, and the form of the disease depends on the timing of the events. *P. vivax* and *P. ovale* complete an erythrocytic cycle every 48 hours, so causing a rise in temperature every third day, giving benign tertian fever. *P. malariæ* takes 72 hours, and gives a quartan fever, while *P. falciparum* is less regular and causes malignant tertian or quotidian fever. Many generations of parasites succeed one another, until, if the patient does not die, his reaction causes the parasite to die out. He then recovers, but, if he has been infected with *P. vivax*, *P. ovale*, or *P. malariæ*, he may suffer a relapse after weeks, months, or years, and parasites can again be found in the blood. This is because some of the schizozoites, liberated at the end of the pre-erythrocytic cycle, do not invade the blood, but enter liver cells and start a new cycle there. This, now called exoerythrocytic, to distinguish it from the primary

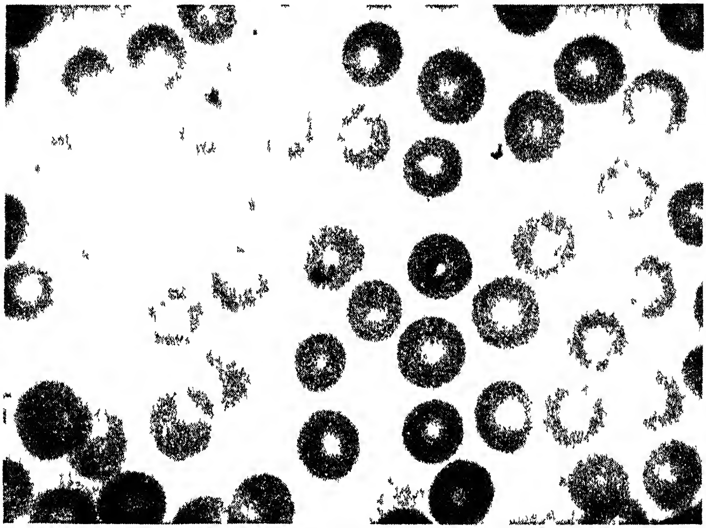


FIG 68 — *Plasmodium vivax* Ring shaped trophozoites in human red blood cells × 1 000 —Photograph by Prof J F D Shrewsbury

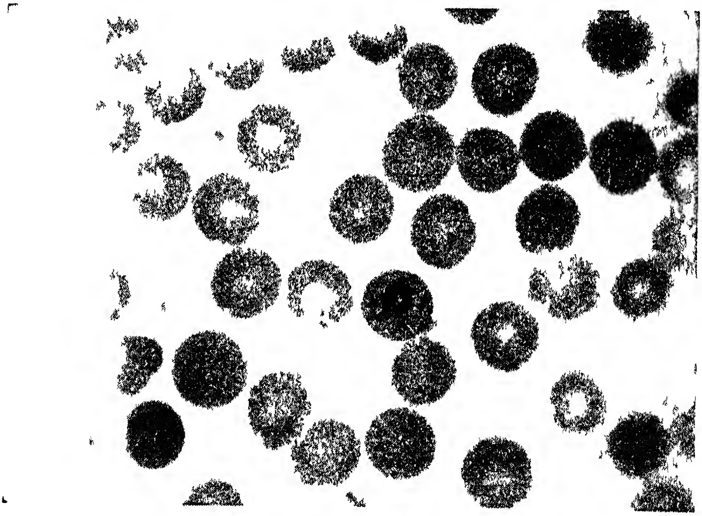


FIG 69 — *Plasmodium falciparum* Developing trophozoite in human red cell × 1 000 —Photograph by Prof J F D Shrewsbury

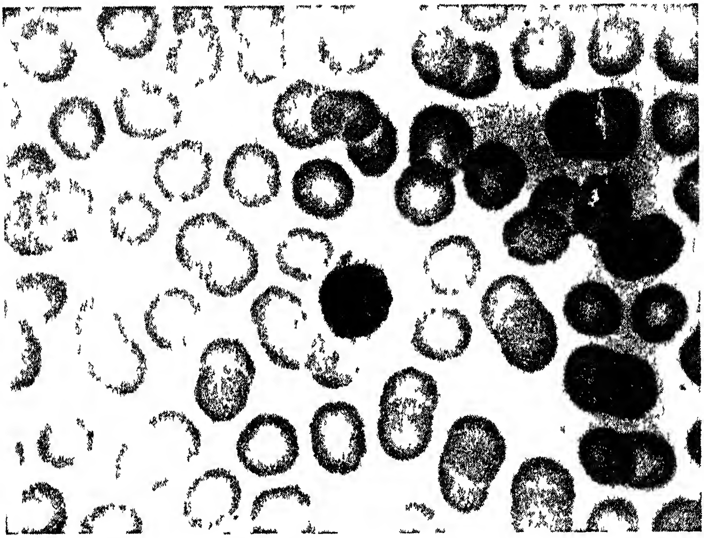


FIG 6 10 *Plasmodium vivax* Merozoite × 1 000—Photograph by Prof. J F D Shrewsbury

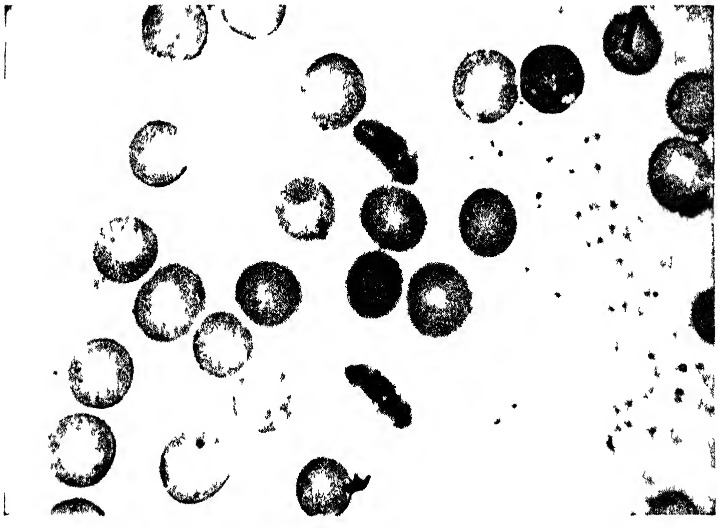


FIG 6 11—*Plasmodium falciparum* Crescentic gamonts × 1,000—Photograph by Prof J F D Shrewsbury

cycle in the liver, may be repeated, and since the cycle in the liver causes no clinical symptoms, its existence went long undetected. Eventually the blood may be invaded, probably because the host's acquired immunity has waned, and the disease is again apparent. *P. malariæ* differs from the others in giving no short-term relapses, but in persisting for very many years. Whether, in such cases, the parasites in the liver have been active in schizogony (the production of schizozoites) all the time, or have persisted in a quiescent state, is unknown. The exoerythrocytic cycle has not been detected in *P. falciparum*, and almost certainly does not occur.

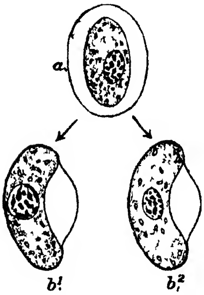


FIG 6 12 Gamonts of *Plasmodium falciparum*

a, Before taking on the sausage shape, *b*¹, male gamont in sausage stage, *b*² female gamont in the same stage The outline is that of the red corpuscle

After several generations of schizogony in the blood, some of the parasites grow, not to schizonts, but to a new form, the gamont. (It is also known as the gametocyte, a term which, although it is still widely used in medicine, is best avoided owing to its somewhat different meaning in metazoan histology [p. 700].) The gamonts of *P. falciparum* are sickle-shaped (hence their trivial name), those of the others rounded. They are larger than the schizonts, and have more of the dark pigment. They develop no further in the human host.

If the blood of a malarial patient is sucked by the right sort of gnat further development takes place. The gnat must be of the genus *Anopheles*, but not all species of the genus are carriers of malaria, and different species are important in different countries. While other stages of the parasite are digested in the gnat's stomach, the gamont, set free from the human blood cell inside which it lives, forms gametes. It is either female, in which case the nucleus divides twice, much as in the formation of polar bodies in an egg (p. 702), so that some nuclear material is lost and a single large female gamete is formed, or male, in which case the nucleus divides rapidly into some half-dozen parts, which come to the surface and protrude from the cell as threads of nucleoplasm surrounded by a very thin sheath of cytoplasm. They lash violently until they break free from the main mass of cytoplasm, which dies. They are then male gametes, each of which may undergo syngamy with a female gamete.

All this has taken place in the lumen of the insect's gut. The zygote changes to an active, slightly elongated shape, when it is known as an ookinete, and bores into the lining of the gut, coming to rest in the subepithelial tissue. Here it rounds off and becomes a sporont, which absorbs food from its host, and grows, forming a blister on the posterior part of the wall of the midgut (Fig. 6.13). While it grows, the nucleus divides repeatedly, and most of the cytoplasm becomes aggregated round the daughter nuclei to form a very large number of worm-like sporozoites. The wall of the sporont bursts, some residual cytoplasm is left, and the sporozoites enter the body cavity of the gnat. Some find their way to the salivary glands and are ready to infect a man when the gnat next bites.

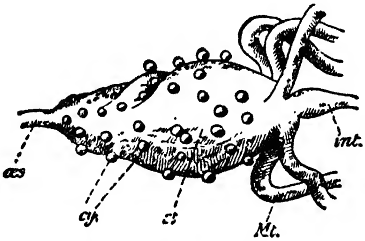


FIG. 6.13.—Part of the alimentary canal of a mosquito infested with *Plasmodium*.—From Lankester's *Zoology*, after Ross.

cy., Cysts of the parasite; *int.*, intestine; *M.t.*, Malpighian tubes; *œs.*, œsophagus; *st.*, stomach.

The occurrence and distribution of malaria depends to a great extent on the existence of suitable habitats for the appropriate gnats. Some of these need large bodies of water, others can breed in small puddles such as those that collect in old tree trunks. The larvæ of all of them (p. 256) can be killed by covering the water in which they live with a layer of paraffin, but this method of control is not of much use for the species that live in small puddles. *P. falciparum* needs a relatively high temperature - about 21° C. in summer and 8° C. in winter—to carry out the part of its life-cycle in the gnat, so that in temperate climates it cannot persist, though travellers may bring it with them and cause short epidemics, especially in summer. In the tropics it is endemic, and all children become infected by the age of 18 months, though after ten years of age they develop a partial immunity. For long the only direct attack on the parasites was by quinine, a drug discovered empirically by the South American Indians; now other and more active synthetic drugs are available, and they can be selected for maximum action on particular species of *Plasmodium* and for different stages in the life-cycle.

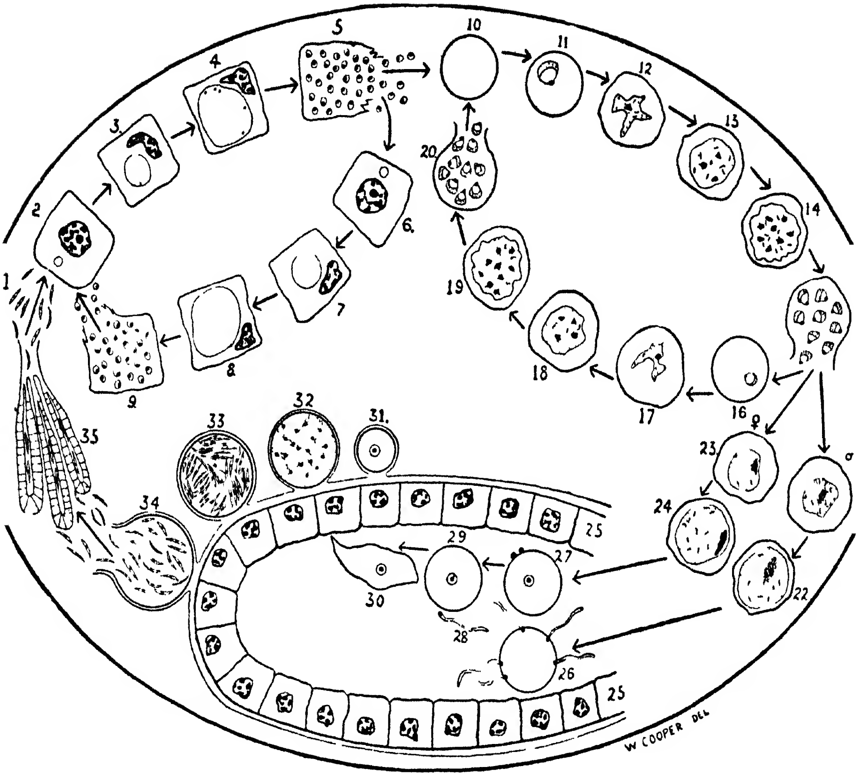
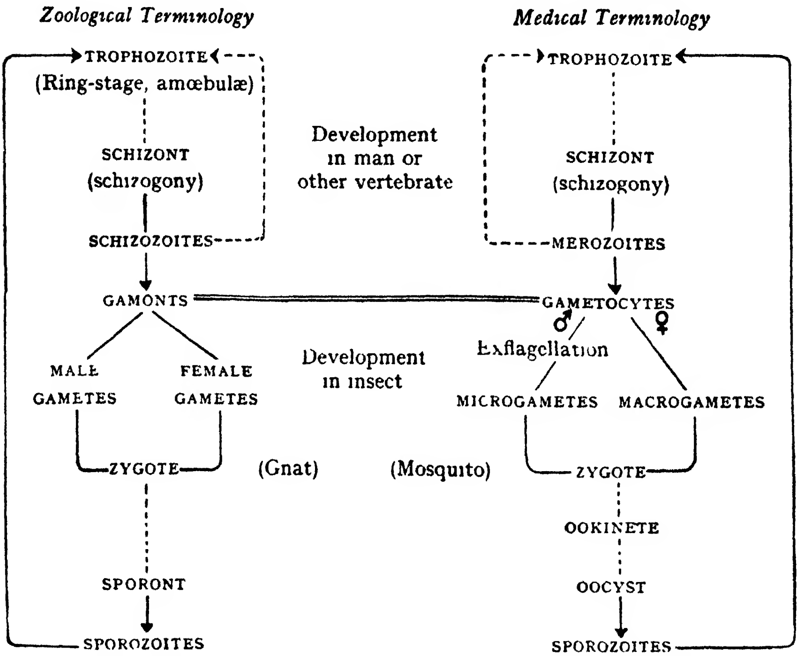


FIG. 6.14.—Diagram of the life cycle of *Plasmodium vivax*, *P. ovale* and probably *P. malariae*; that of *P. falciparum* is similar except that stages 6–9 are omitted. From Shortt, *Trans. roy. Soc. trop. Med. Hyg.*, 1948, 42, 227.

1. Sporozoites from salivary glands of mosquito enter liver cells.
2. Liver cell containing early stage of pre-erythrocytic parasite.
3 and 4. Stages in development of the pre-erythrocytic schizont in liver cells.
5. Fully developed pre-erythrocytic schizont rupturing and releasing pre-erythrocytic schizozoites.
6. Liver cell containing schizozoites of exo-erythrocytic cycle of schizogony.
7–9. Remaining stages in exo-erythrocytic schizogony ending in second generation of schizozoite.
10. Red cell of circulating blood.
11–14. Stages in erythrocytic schizogony in circulating blood.
15. Fully developed erythrocytic schizont rupturing and releasing erythrocytic schizozoites and gamonts.
16–20. Repetition of erythrocytic schizogony.
21–22. Development of male gamont in circulating blood.
23–24. Development of female gamont in circulating blood.
25. Wall of mid gut of mosquito.
26. Exflagellating male gamont producing male gametes in gut of mosquito.
27. Female gamont extruding polar bodies and so becoming a female gamete.
28. Male gamete free in gut of mosquito.
29. Zygote.
30. Ookinete about to penetrate epithelium of gut.
31. Sporont lying under elastic membrane on outer surface of gut.
32–33. Stages in development of sporont with production of sporozoites.
34. Rupture of mature sporont with dispersion of sporozoites.
35. Salivary gland of mosquito containing mature sporozoites.

TERMINOLOGY

The following summary of the life-history of the malaria parasite gives in the left-hand column the terms generally used in zoology, and in the right-hand column those used in medicine. Solid lines represent a reproductive process ; dotted ones development without reproduction.



BALANTIDIUM COLI

The Ciliata are not commonly parasites of man, but *Balantidium coli*, which closely resembles *B. entozoon* (p. 59), may cause serious disease, and even death. It normally lives in the large intestine of the pig, which it appears not to harm, but if the cysts which it forms are swallowed by man, it may penetrate the epithelium of the gut and cause dysentery. It may occasionally be carried in the blood stream to other parts of the body and there cause abscesses. It occurs in all parts of the world.

7

THE CLASSIFICATION OF PROTOZOA

THE one characteristic which the examples that we have discussed have in common is that, whether they have one nucleus or several, no nucleus is separated from another by a cell wall; or, in physiological rather than morphological terms, no nucleus ever exerts its controlling influence on a part only of the cytoplasm. This is true of all the animals which are commonly called Protozoa with the exception of a small group called Cnidosporidia, which have peculiar structures called pole capsules which seem to have their own nuclei. As we have seen, a formal distinction between animal and plant flagellates is impossible, but if we begin by saying that the Protozoa are animals, the criterion of absence of cell walls makes a workable, if not entirely adequate, definition. It avoids the necessity of defining the cell, and so the necessity of deciding whether the Protozoa are all non-cellular or not. It is clear that they are not all unicellular, for all definitions of a cell agree that it has but one nucleus.

At some point, however, we shall have to consider the meaning of the word cell, and it may be said here that the two views which have been current differ rather in their metaphysical outlook than in their morphological terminology. According to one view, a cell is a part of an organism, and as such it can have no fundamental similarity to a protozoan such as *Trypanosoma*. The other view, which looks on uninucleate Protozoa as being single cells, is historically connected with the evolutionary view that all other animals are derived from Protozoa by a series of fissions after which the daughter units remained in contact, as they do in the embryology of higher forms (Chap. 28). However probable on general grounds one may choose to consider this hypothesis, there is not a single piece of evidence for it, and it is therefore unwise to make much of it. As was first stressed by Dobell, a protozoan carries out all the ordinary activities of the so-called higher animals, and differs from them only in the organs used; our increased knowledge now makes this even clearer. For some reason or other *Amœba* is generally venerated as the first ancestor of all animals, but for this view also there

is no evidence. As Dobell wrote in 1911 of this universal parent:

> 'Concerning this fabulous "amœba" we know nothing, save that its correct systematic position is probably in the group which contains the centaur, the phœnix, and the hippogriff.'

If the Protozoa are indeed the first animals, one can be fairly confident that the primitive form was flagellate rather than amœboid, for it is the flagellate forms which connect most closely with plants.

The Protozoa contain, in addition to the various organelles described in the preceding examples, all of which the student may hope to see for himself, various other structures that can be demonstrated satisfactorily only with the help of the electron microscope. Mitochondria (p. 29) are generally present, and there are often other structures with a double membranous wall, called variously granular membranes, dictyosomes and kinetoplasts.

The group Protozoa is a phylum, but it is sometimes also raised to the rank of a sub-kingdom, the only other sub-kingdoms being the Parazoa or sponges (p. 81), and the Metazoa, including all other animals. All modern writers are agreed on the main divisions of the Protozoa, but there is some variation in the names used.

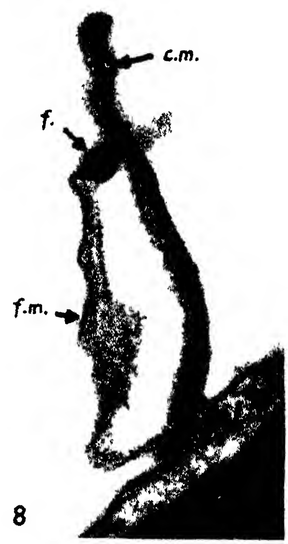


Fig. 7.1.—Electronmicrograph of a transverse section through the undulating membrane of *Trichomonas*, showing its formation from a fold in the cell membrane (c m.) and a flagellum with an enormously expanded membrane (f m.): the 9+2 bundles of the flagellum are visible at f. × 64,000.—From Grimstone, *Biol. Rev.*, 1961. 36, 97.

CLASS I.—MASTIGOPHORA

Protozoa which are predominantly flagellate although they may form pseudopodia. Binary fission is longitudinal, so that the daughters are nearly symmetrical, although one retains the original flagellum while the other grows a new one. The division of the basal

granule is usually the first sign of division, and it often acts as a centriole. It is best to avoid the name Flagellata as a title for this group, since the word is used by botanists with a different and wider connotation. There are two sub-classes—Phytomastigina, which possess chlorophyll or closely resemble forms which do; and Zoomastigina, which neither possess chlorophyll themselves, nor resemble forms which do. Most of the Phytomastigina, such as *Polytoma* and *Euglena*, are on the border line between the animal and plant kingdoms ; others, such as *Chlamydomonas*, have no claim to be called animals, and are only included, by some zoologists, as Mastigophora because of their structural similarity to colourless forms. The biochemistry of the sub-class is diverse, which suggests that they are not closely related to each other, and there is some evidence that they are degenerate Algæ. The Zoomastigina, on the other hand, are entirely animal in nature, and have little or nothing in common with the Phytomastigina except flagella. Syngamy is rare. Many have a somewhat complicated internal structure of nuclei, skeletal rods, fibres and so on, and many also have several flagella. *Trypanosoma* is an example with one flagellum, *Trichomonas*, parasitic in the gut, has several.

CLASS II.—RHIZOPODA

Protozoa which have pseudopodia for most of their life histories, and flagella, if at all, in young stages only. Besides forms like *Amœba* and *Entamœba* (Order Amœbina) there are others with

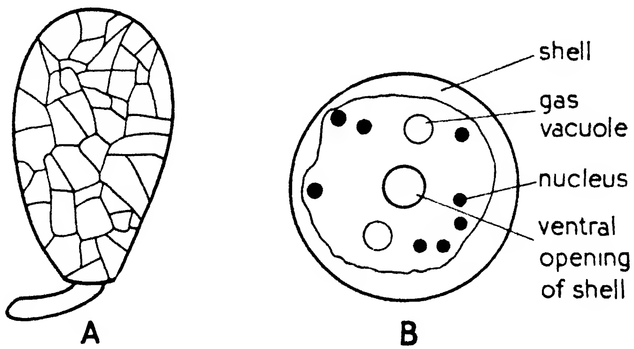


FIG. 7.2.—Testacea.

A, *Difflugia* ; living individual, showing shell of sand grains and one pseudopodium ; *B*, *Arcella* ; stained individual with eight nuclei, dorsal view, the opening of the shell is seen through the cytoplasm.

blunt pseudopodia and shells (Testacea, Fig. 7.2), with shells and reticulate pseudopodia (Foraminifera), and with fine radial pseudopodia (Radiolaria). In the order Heliozoa the pseudopodia, known as axopodia, have a central axis of close-packed fibres, surrounded by a vacuolated sheath. Flagellate gametes are common throughout the orders Foraminifera and Radiolaria, and some genera such as *Dimastigamœba* and *Hartmanella* which live

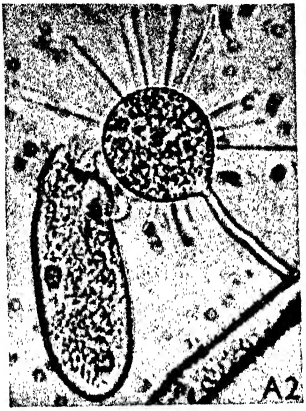


FIG. 7.3.—A suctorian (*Podophrya*) feeding on the ciliate *Colpidium*—From Kitching, *J. exp. Biol.*, 1952, 29, 255.

in soil may, when water is added to them, withdraw their pseudopodia and form two (or one or three) flagella by means of which they swim. In this state they neither feed nor divide, and they revert to the amœboid form after a few hours.

CLASS III.—SPOROZOA

This group is rather a waste-paper basket for parasites which have no organs of locomotion except in young or distributive stages, and includes forms of no particularly close relationship. Many are intracellular in habitat at some stage in their life-history. Examples are *Monocystis* and *Plasmodium*. The Cnidosporidia, the only Protozoa with cells, are put here, though whether they belong here is another matter.

CLASS IV.—CILIOPHORA

Protozoa with nuclei of two types, one concerned with somatic matters and the other with syngamy, and cilia at some stage of

the life-history. Reproduction is by fission which cuts across the lines of cilia, so that it is usually transverse and the daughter cells are initially very different from each other, and by conjugation of the type we have seen in *Paramecium*. The typical ciliates bear cilia throughout life and are subdivided by the way in which they are arranged. In the Suctoria (Fig. 7.3) the adults lose their cilia and replace them by tentacle-like structures. *Opalina* and a few other genera have a number of nuclei which are all alike. *Opalina*, does not, however, undergo the typical ciliate conjugation, and is placed by some zoologists in the Mastigophora. The cilia of Ciliata have a similar structure to those of Metazoa (p. 506), but can reverse their direction of beat, which those of Metazoa other than cœlenterates never do.

On account of the difference in the nuclei some protozoologists feel that the Ciliophora should be raised to the rank of a subphylum, to which the name Heterokaryota has been given. When this is done the other three classes may be united as Subphylum Homokaryota.

8

SPONGES

A SIMPLE SPONGE

The structure of sponges is best understood by considering the Olynthus, which is found only as a fleeting stage in the development of a few members of the group. It is a hollow vase, perforated by many pores, and having at the summit a single large opening, the osculum. Through the pores water constantly enters it, to pass out through the osculum. Herein the sponges differ from all other animals, using the principal opening not for intaking—as a mouth—but for casting out. The wall of the vase consists of two layers (Fig. 8.2) ; the inner is composed of collared flagellate cells, or choanocytes, standing side by side but not touching, and resembling the choanoflagellates (p. 38). The collars appear not to be continuous sheets of protoplasm but to consist of a network of fibrils. The outer or dermal layer makes up the greater part of the thickness of the wall and is turned in a little way at the rim. This layer again consists of two parts, a covering layer of flattened cells, known as pinacocytes, which have the power of changing their shape, and the skeletogenous layer, between them and the gastral layer. The skeletogenous layer consists of scattered cells, embedded in a jelly of collagen. The most numerous of these cells are engaged in secreting spicules of calcium carbonate by which the wall is supported. They wander from the covering layer into the jelly, and then each divides into two, and the resulting pair secrete in their protoplasm, which is continuous, a needle-like spicule which presently outgrows them. Most often the original spicule cells come together in threes before this process, so that the three spicules which they secrete become the rays of a three-rayed compound spicule. This lies in the wall with two rays towards the osculum and one away from it. Sometimes a fourth cell joins the others later, and forms a fourth ray which projects inwards towards the internal cavity paragaster. Often there are simple spicules which project from the surface of the sponge. Other cells, known as porocytes, of a conical shape, extend through the jelly, having their base in the covering layer while their apex reaches the paragaster between the choanocytes. Each is pierced from

base to apex by a tube, which is one of the pores. Besides these cells of the dermal layer there are in the jelly wandering amœboid cells which appear, in some cases at least, to belong neither to the gastral nor to the dermal layer, but to be descended independently from blastomeres of the embryo. Some of them become ova; others, it is believed, give rise to male gametes; the rest are occupied in transporting nutriment and excreta about the sponge. The current which flows through the body is set up by the working of the flagella of the choanocytes. It carries with it various minute organisms which serve the sponge for food, being swallowed, in some way which is still in dispute, by the collar cells. These digest the food, rejecting the indigestible parts into the space within the collar, and passing on the digested food to amœbocytes, which visit them to obtain it.

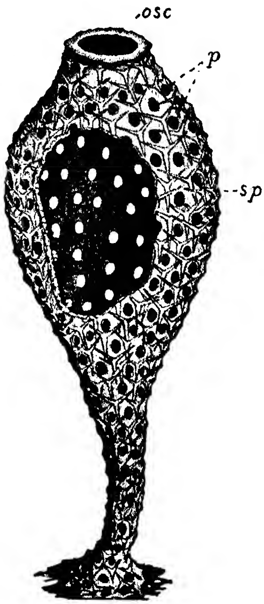


FIG. 8.1.—The Olynthus stage of a calcareous sponge, from which a portion of the wall has been removed to expose the paragaster.

osc., Osculum; *p.*, pores; *sp.*, spicule in wall.

COMPLEX SPONGE BODIES

No sponge remains at this simple stage throughout its life. At the least the body branches and thus complicates its shape, and then often new oscula appear at the ends of the branches. A higher grade is reached when, as in the calcareous sponge *Sycon*, the greater part of the vase is covered with blind, thimble-shaped outgrowths, regularly arranged, and touching in places, but leaving between them channels, known as inhalant canals, whose openings on the surface of the sponge are often narrowed and are known as ostia. The thimble-shaped chambers are known as flagellated chambers, and are lined by choanocytes, but these are now lacking from the paragaster, where they are replaced by pinacocytes. Water enters by the ostia, passes along the inhalant canals and through the pores, now known as prosopyles, into the excurrent canals, leaves these through the openings, known as apopyles, by which they communicate with the para-

gaster, and flows outwards through the osculum. A third grade is found in sponges such as the calcareous sponge *Leucilla*, where

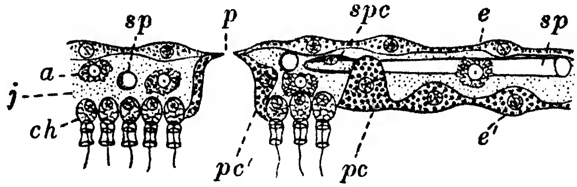


FIG. 8.2.—Part of a longitudinal section of the wall of an Olynthus, including a portion of the rim of the osculum.

a, Amœboid cell ; *ch.*, choanocyte ; *e*, flat covering cells (pinacocytes) of dermal layer ; *e'*, similar cells lining the rim of the osculum ; *j*, jelly ; *p*, pore ; *pc.*, young porocyte ; *pc'.*, fully developed porocyte ; *sp*. spicule ; *spc.*, spicule cell.

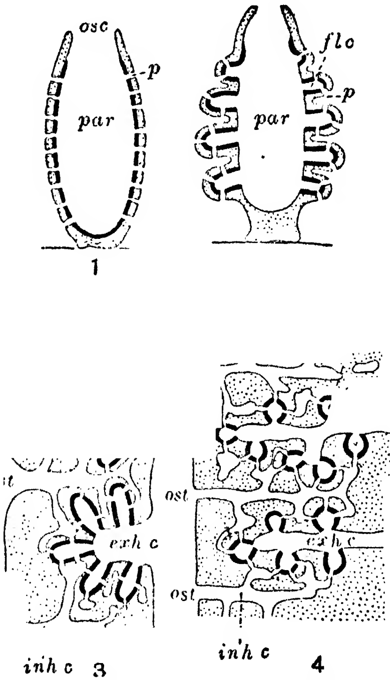


FIG. 8.3.—Diagrams of the canal system of sponges.—Partly after Minchin.

exh.c., Exhalant canal ; *inh.c.*, inhalant canal ; *fl.c.*, flagellated chamber ; *osc.*, osculum ; *ost.*, ostium; *p.*, pore ; *par.*, paragaster.

the wall of the paragaster is folded a second time, so that the flagellated chambers, instead of opening direct into the paragaster, communicate with it by exhalant canals lined with pinacocytes

The three grades of sponge structure, in which successively

the choanocytes line the whole paragaster, are restricted to flagellated chambers, or are still further removed by the presence of exhalant canals, are known as the 'Ascon', 'Sycon', and 'Leucon' grades. As the canal system has grown more intricate, complication has taken place also in the skeletogenous layer. It has grown thicker, forming outside the flagellated chambers a layer known as the cortex, in which the inhalant canals ramify; and there appear in it branched connective tissue cells which can change their shape.

SILICEOUS AND HORNY SPONGES

The examples of which we have so far spoken have calcareous skeletons, but most sponges have a skeleton of siliceous spicules. In all these the canal systems are of one of the more complicated types, and usually they are made still more intricate by ramifyings of the paragaster, and the appearance of numerous oscula, which put it into communication with the water at many points. The bath sponges belong to a small group in which the skeleton

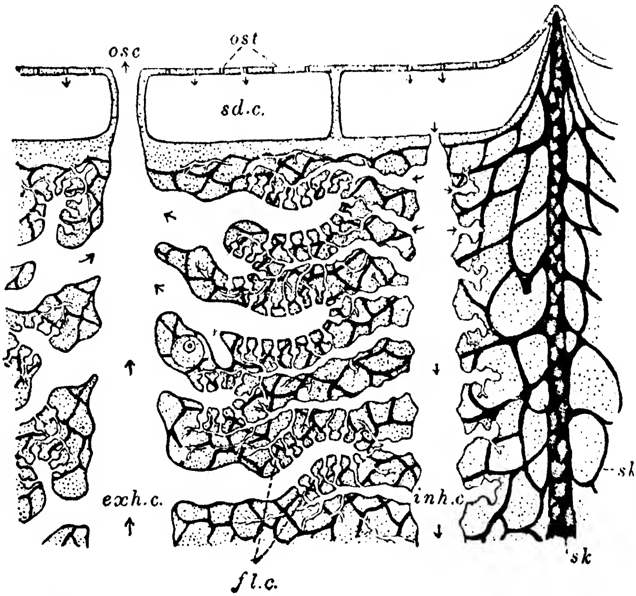


FIG. 8.4.—A diagram of the structure of a bath sponge.

exh.c., Exhalant canal; *inh.c.*, inhalant canal; *fl.c.*, flagellated chamber; *osc.*, osculum; *ost.*, ostium; *sd.c.*, subdermal cavity; *sk.*, one of the principal pillars of the skeleton, containing embedded sand grains; *sk'.*, minor fibres of the skeleton.

is not spicular but a network of fibres of spongin, usually strengthened by sand grains embedded in the fibres. Their canal system is of the type which has small, round chambers. When the sponge is prepared for human use, the soft parts are allowed to die and rot, leaving the skeleton, which is then cleaned. The large holes on the upper part of the dried skeleton mark the position of the oscula ; in its interstices formerly lay the ramifications of the canal system. The true bath sponge (*Euspongia officinalis*), which has very few particles of sand, is gathered in 10 to 15 fathoms of water, the finest varieties from the Adriatic, coarser ones from elsewhere in the Mediterranean, the West Indies, and Australian seas. Various species of *Hippospongia* yield coarse kinds of sponge.

Sponges have free larvæ, of several different kinds, but all are covered with flagellate cells, by which they swim. The remarkable feature of the metamorphoses by which these larvæ become the fixed adults is that the flagellated cells pass into the interior, develop collars, and become the choanocytes.

PORIFERA: GENERAL FEATURES

The majority of sponges are marine, and the group is best developed in warmer seas. A few species are British, and *Spongilla*, one of the few fresh-water forms, occurs in our lakes and rivers.

The sponges are known in zoology as Porifera. In that their bodies consist of many ' cells ', they might seem to be Metazoa. But they differ from all members of that group in several important respects. In no metazoan are choanocytes found. In none is the principal opening exhalant. In none is there during development an inversion whereby a flagellated outer covering becomes internal. Lastly, and perhaps most significantly, in a sponge the ' cells ' are far less specialised and dependent upon one another than the cells of a metazoan. Many of them can assume various forms, becoming amœboid, collared, etc. Many are isolated in the jelly, and when they touch there is no cytoplasmic continuity. There is no nervous system. Even the choanocytes, though their efforts together produce a current, do not keep time in their working. In short, the Porifera are practically colonies of Protozoa. For these reasons it is best that, in a classification of animals, they should be given the same rank as the Protozoa and Metazoa : when this is done, they are known as phylum Porifera, sub-kingdom Parazoa.

9

HYDRA AND THE CŒLENTERATES

HYDRA

IF a handful of weeds gathered from a freshwater pond be placed in a beaker of water and allowed to stand for a while, there will often be found hanging from the sides of the beaker or from the weeds some short threads of a green, brown, or whitish colour. By one end each thread sticks to the glass. At the other it bears about half a dozen finer threads, which hang down in the water if they be left undisturbed. A touch will cause these to be withdrawn and take on a shorter and thicker shape, and a stronger blow will cause the whole structure to contract into a subspherical knob, surmounted by a crown of smaller knobs. It is clear that these objects are living beings: in point of fact each of them is a specimen of the animal known as *Hydra*. According to their colour and other characters they have been divided into a number of species and subgenera. *Chlorohydra viridissima* (=*H. viridis*) is green. *Hydra oligactis* (=*H. fusca*) is brown and has a stalk, and tentacles up to 25 cm. long; and *H. attenuata*, also brown, has no stalk, and the tentacles are only twice the length of the body. The following account applies in general to all of them.

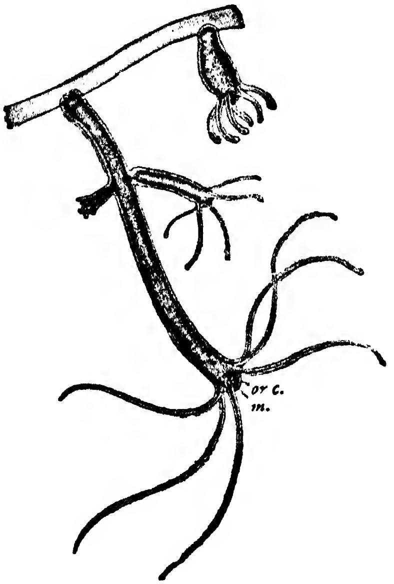


FIG. 9.1.—Two specimens of *Chlorohydra viridissima* × *c.* 6, one contracted, the other in a state of moderate expansion, the latter bearing two buds in different stages.

m., Mouth; *or.c.*, oral cone.

SHAPE

The body of *Hydra* is a hollow cylinder, with a ring of hollow outgrowths or tentacles surrounding an opening or mouth at one end, and the other end closed by a flat basal disc or foot. The mouth is raised upon an oral cone or hypostome; it leads into the cavity of the cylinder, with which the hollows of the tentacles are continuous. This space is the enteron. The cylinder is rather wider in the middle than near the ends. The wall of the body is composed of two protoplasmic layers (Fig. 9.2), the outer known as the ectoderm and the inner as the endoderm, with a mesogloea between them, consisting of a gelatinous substance, with an indistinct fibrous structure, which they secrete. Such a body as this is known as a polyp, because of its superficial resemblance to an octopus (Latin *polypus*, having many feet).

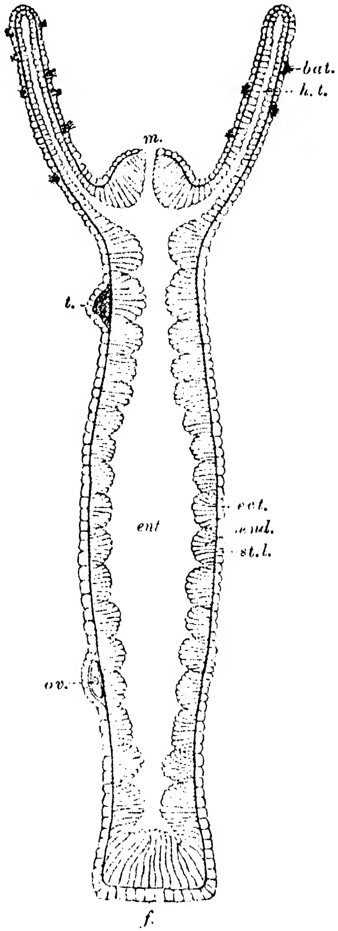


FIG. 9.2.—A diagrammatic, longitudinal section of *Hydra*, magnified. —From Shipley and MacBride.

bat., Battery of nematocysts. Only a few of these are shown; they cover the tentacles; *ect.*, ectoderm; *end.*, endoderm; *ent.*, enteron; *f.*, foot; *h.t.*, hollow of a tentacle; *m.*, mouth; *ov.*, ovary; *st.l.*, structureless lamella; *t.*, testis.

ECTODERM

The ectoderm consists of several kinds of cells (Fig. 9.4), of which the most conspicuous are those known as musculo- or myo-epithelial cells. These have broad outer ends, which meet and form the surface of the body, standing on several pillars which reach and expand upon the mesogloea, where each cell is generally considered to be drawn out into one or more contractile processes. The processes, each containing a

fibre, run along the cylinder and tentacles, at right angles to the cell, forming a distinct layer on the outer side of the structureless lamella. Over the greater part of the body the surface layer of the protoplasm is a firm pellicle, but in the disc this is absent. The cells in this region are also peculiar in containing granules of a substance secreted by the protoplasm which is used to fix the animal to the surface it hangs from. Each musculo-epithelial cell has a large oval nucleus in one of its pillars. In the tentacles these cells are less tall than elsewhere. Between the pillars are spaces which contain small, rounded interstitial cells. These form a reserve from which, in various circumstances, any of the other cells of the body can arise and they thus retain the undifferentiated nature of the germ cells. Between the pillars stand also peculiar cells known as cnidoblasts, which project through the surface protoplasm. These are very numerous in the tentacles, where they lie in groups or batteries (Fig. 9.2), but absent from the basal disc. Each of them has a pear-shaped body with the narrow end at the surface of the animal, where there projects from it a short process known as the cnidocil. On this side the cell contains a pear-shaped sac, called the nematocyst, with a lid, the operculum. The narrow outer end of the sac is tucked in and produced into a long, hollow thread, which lies coiled up in the sac. The space between the thread and the wall of the sac contains a fluid. On stimulation the thread is expelled, being turned inside out in the process, but little is known of how this is brought about. There is no nervous control and there is no evidence for the common statement that the cnidocil is a sense organ. The nematocysts are discharged by tactile stimuli preceded by a chemical stimulus, the latter facilitating the effect of the former, and a strong mechanical stimulus is effective by itself. Bursting of the operculum is probably caused by the absorption of water. The nematocysts are of four kinds—a large kind with a straight thread provided with barbs at the base, a small kind with a spiral thread and reduced spines, and two other small kinds with a

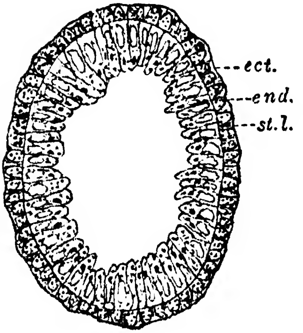


FIG. 9.3.—A transverse section of *Hydra*, stained and seen under the low power of the microscope. × *c.* 120.

ect., Ectoderm ; *end.*, endoderm; *st.l.*, structureless lamella.

straight thread and a narrower sac than the others, one of which has spines while the other has not. The broad end of each cnidoblast is anchored into the body by a process which runs inward to the mesogloea. The tentacles are covered with a

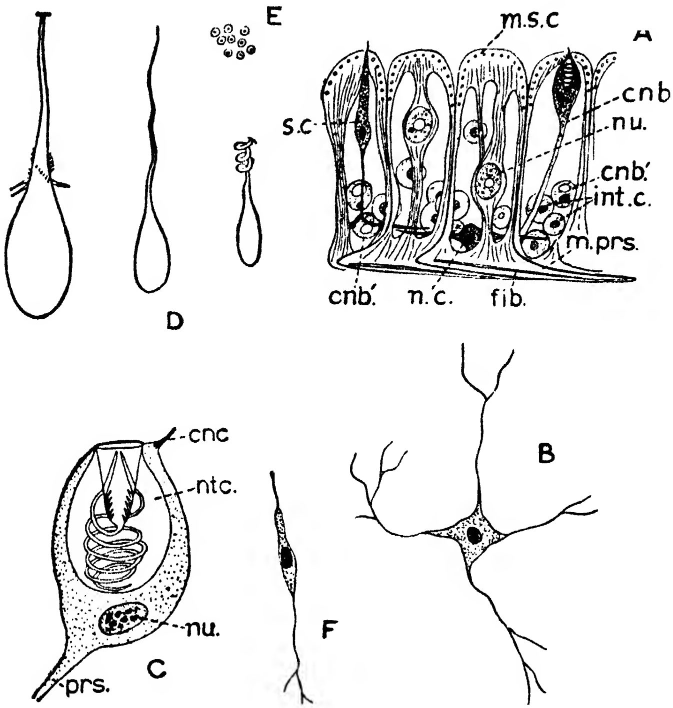


FIG. 9.4.—The histology of *Hydra*.

The figures are diagrammatic and not drawn to scale.

A, Musculo-epithelia cells; *B*, a nerve cell; *C*, a cnidoblast; *D*, nematocysts of three kinds; *E*, zoochlorellæ; *F*, a sense cell.

cnb., Cnidoblast; *cnb'.*, interstitial cell which will become a cnidoblast, with vacuole for nematocyst; *cnc.*, cnidocil; *fib.*, fibre; *int.c.*, interstitial cell; *m.prs.*, contractile process; *m.s.c.*, musculo-epithelial cell; *n.c.*, nerve cell; *ntc.*, nematocyst; *nu.*, nucleus; *prs.*, basal process of the cnidoblast; *s.c.*, sense cell.

number of wart-like knobs, each consisting of a large musculo-epithelial cell, in which is sunk a battery of cnidoblasts consisting of one or two of the large kind with several of the smaller kinds around them. Each of the kinds of nematocysts has a function of its own. The large, barbed nematocysts are weapons of offence and perhaps also of defence. When they are discharged, their barbs emerge first and make a wound in the tissues of the prey, into

which the thread is driven (Fig. 9.5) and through the hole so made tissue-fluid escapes and induces swallowing (p. 95). In piercing the chitin of arthropods, upon which the *Hydra* feeds, the nematocysts are assisted by the corrosive action of a fluid which they contain, either in the hollow of the tucked-in thread or in that of the sac. This fluid also temporarily numbs the prey, and the barbs hold it until it is swallowed. In this the spiral kind possibly assist by coiling round bristles upon the body of the

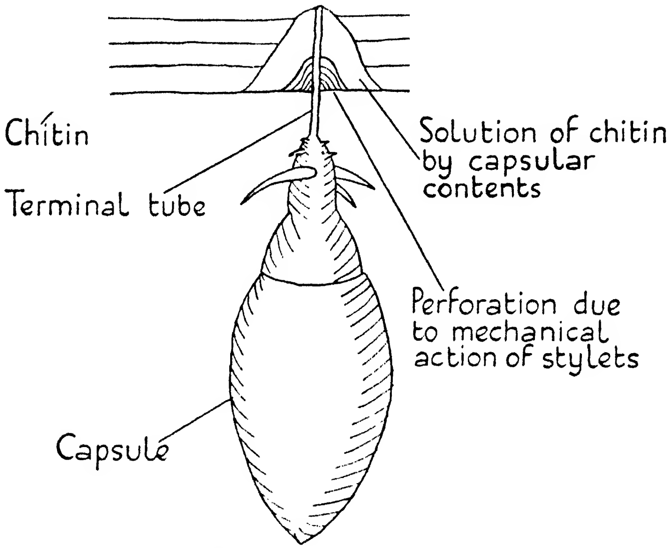


FIG. 9.5.—Nematocyst of *Hydra* with the tube perforating the chitin of an arthropod.—From Yapp, after Toppe. Yapp, *An Introduction to Animal Physiology*, 1939. Clarendon Press, Oxford.

prey, while the other nematocysts are perhaps of use in attaching the tentacles of the hydra, either to its prey or to other objects, by the stickiness of their threads. The cnidoblasts arise from the interstitial cells by the formation of a vacuole and its gradual modification into a nematocyst. They are formed in the upper region of the cylinder and migrate thence to various parts ofthe body, where they take up their position in the outer layer. The germ cells also arise in the ectoderm from the interstitial cells by a process which we shall describe later. Lastly, among the bases of the ectoderm pillars lies a mesh-work of branching nerve cells which is joined by rootlets from tall, narrow sense cells that,

like the cnidoblasts, pierce the surface protoplasm. How these cells are connected is not certain ; probably it is not by continuity of their processes but, as in the synapses of higher animals (p. 514), by contiguity.

The function of a nervous system is to conduct impulses started in it by sense organs, and thus to co-ordinate the movements and reactions of the body. Fundamentally all nervous

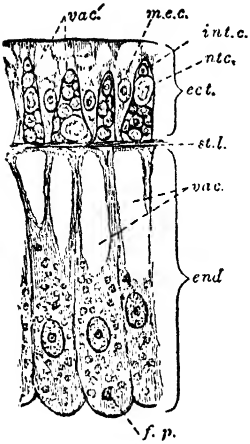


FIG. 9.6.—A small portion of a transverse section of *Hydra*. × *c*. 500.

ect., Ectoderm ; *end.*, endoderm *f.p.*, food particle, ingested by an endoderm cell ; *int.c.*, interstitial cells ; *m.e.c.*, musculo-epithelial cell ; *ntc.*, nematocyst ; *st.l.*, structureless lamella ; *vac.*, vacuoles in endoderm cells ; *vac'.*, vacuoles in ectoderm cells.

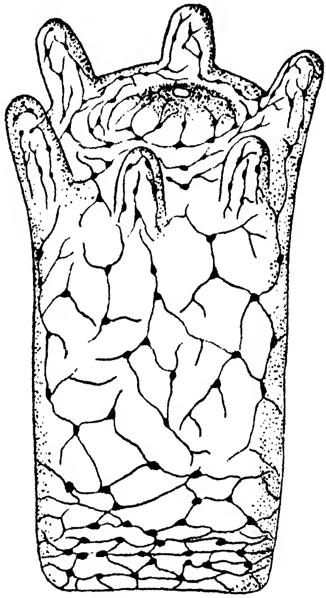


FIG. 9.7.—A diagram of the nervous system of *Hydra*.—After Hadzi.

systems work in the same way, but that of *Hydra* differs in some respects from those of most other animals. The nerve cells form a network, in which it is impossible to distinguish either nerves or a central nervous system, such as vertebrates possess. Impulses travel in the network equally well in all directions, and it is therefore difficult to see how variation in behaviour is possible, but there is in fact some. Most of our knowledge of the physiology of the nerve net is based on that of the sea anemones (p. 111), but there is no reason to think that *Hydra* is greatly different. A stimulus, such as a touch, sets up in a sense cell a train or volley of impulses, and the stronger the stimulus the greater their number. Both the nerve-muscle junction, and to a lesser extent the synapse,

are such that the arrival of an impulse which is not strong enough to jump across makes it easier for the next impulse to do so, a phenomenon known as facilitation. The result is that a strong stimulus affects more muscles than does a weak one, and in particular it affects muscles at a greater distance, as is very obvious when a tentacle is touched. A further result of facilitation is that a repeated weak stimulus may have the same effect as a single stronger one. Both the sense cells and the muscles vary in their sensitivity from time to time, so that the animal does not

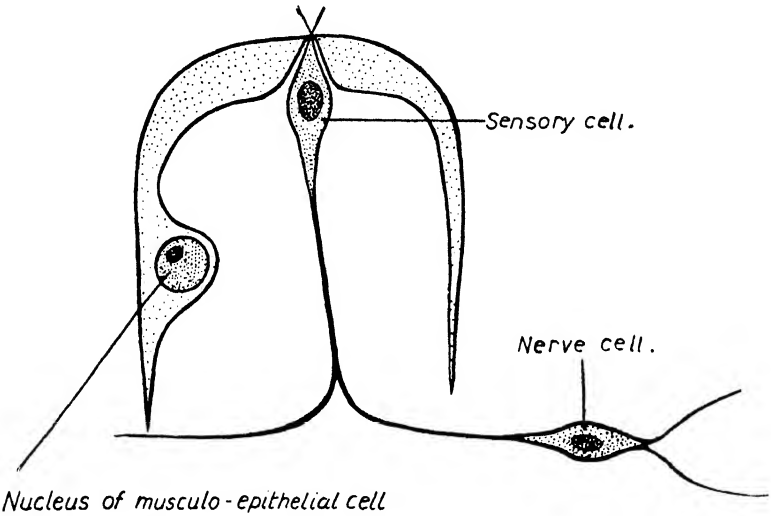


FIG. 9.8.—Sensory cell protruding through a musculo-epithelial cell of *Hydra oligactis*. × 600.—Redrawn from McConnell.

always react in the same way to the same stimulus. A well-fed hydra, for instance, cannot easily be induced to give the feeding reaction (p. 95), and repeated stimulation induces fatigue. This primitive type of nervous system allows of much less precise movements than that in which a particular sense organ is preferentially connected with a particular muscle by means of a nerve. So far as is known, the sense cells are not specialised to serve particular senses, but this, as we shall see later, is largely true even of the sense cells (as distinct from the sense organs) of man.

A description of the behaviour of *Hydra* condensed for a text-book necessarily gives the impression that it is a somewhat rigid matter of responses to stimuli, but a little observation of the creature under the microscope will show that there is both much

spontaneity and much individual variation. Indeed, a great difficulty in experimental work with *Hydra* is that one can never be quite certain whether the animal is responding in a particular way to the stimulus one has just given it, or merely doing so because of an internal situation of which one knows nothing. Besides the contraction already described, and the locomotion and feeding mentioned below, there is another reaction in which a tentacle kinks suddenly through a right angle or more, and then slowly straightens.

ENDODERM

In the endoderm the cells are tall and columnar. Some of them, especially numerous in the oral cone and absent from the tentacles, are glandular. They have a narrow stem and a wide end, turned towards the enteron and containing granules of a substance which they secrete. The most numerous and conspicuous cells are nutritive. They are stout, and some have their bases produced into contractile fibres, which are shorter than those of the musculo-epithelial cells and run around the body, not along it. Their protoplasm contains large vacuoles, and also, in the green hydra, a number of round bodies of a green colour, each of which consists of a central mass of protoplasm with a covering containing the green substance known as chlorophyll, to which the colour of plants is due. These bodies multiply by division. In the other species there are no green bodies, but there are present some yellowish bodies of similar shape, in which, however, no structure can be made out. Each endodermal cell bears two flagella, of typical structure (p. 505), which can be replaced by pseudopodia. There are some sense cells and a few isolated nerve cells.

The green bodies, known as zoochlorellæ, are non-flagellate individuals of a minute plant related to *Chlamydomonas*, of the genus *Carteria*. Like other green plants they nourish themselves by building up complex organic compounds from simple inorganic ones (carbon dioxide, water, salts, etc., see p. 18). They presumably obtain these simple substances as waste products of the metabolism of the hydra. It may be that the hydra absorbs from them in return the excess of carbohydrates which they form, and this would account for the absence from them of starch, which is so constantly found in plants. Thus there would be between the two organisms a partnership, in which the animal

benefited by the removal of waste products and the supply of oxygen and possibly of carbohydrates, and the plant benefited by the rich supply of nitrogenous material and carbon dioxide. Such a partnership is known as symbiosis and is in contrast with parasitism, in which one of the partners benefits at the expense of the other.

MOVEMENTS AND REACTIONS

The movements of *Hydra* are carried out mainly by the muscular processes of the cells, though the surface of the basal disc can put forth pseudopodia, and it is possible that by means of these the animal can slowly change its position. The muscular processes of the ectoderm cells, when they contract, make the body shorter and wider ; those of the endoderm make it narrower and longer. The position of rest is one of moderate extension. The green hydra does not remain passive in the absence of stimuli, but, after standing for some time extended in readiness for prey, it automatically contracts either the whole body or the tentacles only, and then extends in a new direction. Thus it explores the whole of its surroundings. From time to time it changes its position. This is done by extending the body and bending it, so that the tentacles touch some neighbouring object and adhere to it by means of the nematocysts with sticky threads. The basal disc is then either withdrawn altogether from the spot to which it was fixed and put down in a new spot close to the tentacles, or caused to glide up to the tentacles. If the base is put down beyond the tentacles the animal may be said to somersault (Fig. 9.9). A hydra responds to every stimulus, except that of food, by contracting. A stimulus applied to one side of the body a number of times causes it presently to move away in some other direction. *Hydra* avoids both too feeble and too strong a light.

NUTRITION AND EXCRETION

The food of *Hydra* consists of small animals, which are caught by the tentacles, and carried by them to the mouth, which then opens and swallows the prey. It is not pushed in by the tentacles. *Hydra* is seldom able to kill water-fleas, though it can swallow them once they are killed, and it can live indefinitely in water in which there are no other animals large enough to be seen

with the naked eye. The brown hydra, when starved, is able to feed on mud. The animal will not feed unless it be hungry. If it be well fed, creatures which swim against the tentacles are allowed to escape, but, if food has been scarce, as soon as the prey has become temporarily attached by the nematocysts to one tentacle the others bend over towards it and help to secure it and push it towards the mouth. If the animal be starving the mere smell of food in the neighbourhood is enough to set the tentacles working, but usually they are not put into action till the food has been both smelt and touched. It is not possible to deceive the hydra into swallowing substances, such as pieces of blotting-

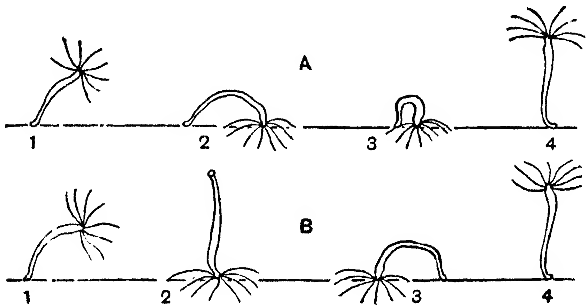
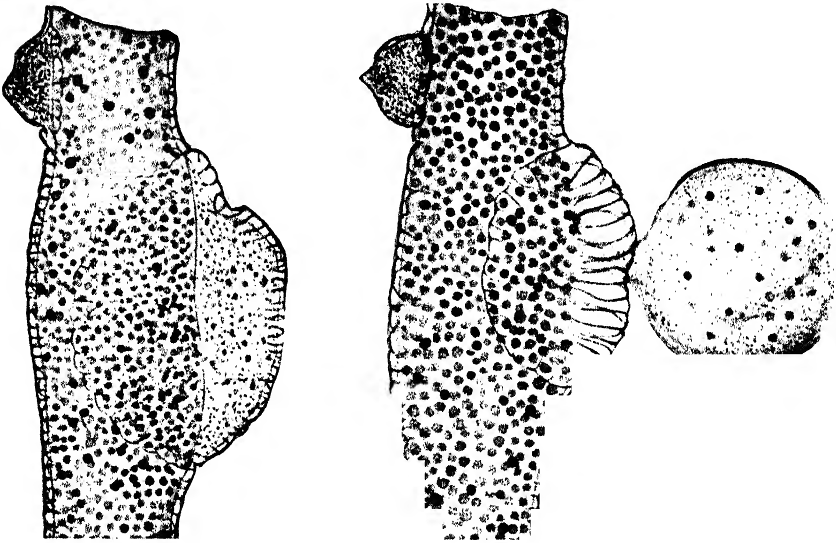


FIG. 9.9.—*Hydra* in the attitudes which it assumes successively in two of its modes of locomotion.

A, 'Looping'; *B*, 'somersaulting'

paper, which do not smell like food, but blotting-paper soaked in beef-tea is swallowed when it touches the tentacles. In some species the substance that induces swallowing is glutathione coenzyme in oxidations), released from the prey by the barbs. Once swallowed, the food is passed deep into the enteron and there softened by a juice which the gland cells secrete, broken up by the churning which it gets as the body expands and contracts, and swept about by the flagella. Part of the food is dissolved in the enteron and absorbed in solution, part of it taken up by pseudopodia of the endoderm cells and digested within their protoplasm. Presumably the ectoderm is nourished by substances passed on from the endoderm, either by diffusion through the structureless lamella or along the fine threads of protoplasm which put the two layers into connection across it. The undigested remains of the food are driven out of the mouth by a sudden contraction of the wall of the body. In unnatural conditions of

culture the animals become liable to depression much like that of *Paramecium*, in which the powers of movement, feeding, and fission are affected and death ensues. Respiration and excretion probably take place from the surface of the ectoderm and endoderm ; there is no special organ for either process.



A B

FIG. 9.10.—Reproductive organs of the green hydra.

In each case a testis is shown above, to the left, and an ovary below, to the right. In *A* the ovum is unripe, in *B* it is ripe, has burst its covering of ectoderm cells, and hangs by a stalk. The large round spots in the ovum are zoochlorellæ.

REPRODUCTION

The species of *Hydra* reproduce themselves both sexually and asexually. The green form is hermaphrodite, often protandrous, but the two British brown species have the sexes separate. *H. oligactis* usually reproduces sexually in the autumn, the other two in spring and summer. The generative organs are ectodermal structures developed when sexual reproduction is about to take place (Fig. 9.10). The ovaries, of which there is generally only one in each individual, are found in the lower part of the body; the testes, of which there are several, are in the upper part. In the early stages of both organs the interstitial cells multiply and push out the musculo-epithelial cells so as to form a swelling.

In the ovary one of the interstitial cells becomes an oocyte. This increases in size and begins to throw out pseudopodia, by which it swallows the rest of the interstitial cells contained in the swelling. At the same time it lays up in its protoplasm numerous dark, spherical granules of yolk. As the swelling increases, the musculo-epithelial cells are stretched, their conical bodies forming long stalks, which are pushed apart by the oocyte, their outer layer forming a thin covering for the latter. When the oocyte has swallowed all the surrounding cells it withdraws its pseudopodia and becomes a large rounded body, about which a gelatinous coat is secreted. Polar bodies (p. 632) are now formed, the covering of musculo-epithelial cells parts and shrinks back so that the ovum is exposed save for the gelatinous coat, and fertilisation is effected by one of the spermatozoa which are present in the surrounding water. In the formation of a testis the multiplication of the interstitial cells stretches the musculo-epithelial cells as in the ovary. The interstitial cells become spermatocytes, which lie among the stalks of the musculo-epithelial cells and undergo two divisions, the resulting cells developing into spermatozoa with a conical head, a neck, and a tail. By the breaking of the covering layer the spermatozoa are set free and swim in the water, where they perish unless they find a ripe ovum. Since in the green hydra the testis generally ripens first, cross-fertilisation will usually take place, but it does not appear that self-fertilisation is always impossible in this species.

DEVELOPMENT

After fertilisation the egg undergoes cleavage into blastomeres (p. 636), which as they increase in numbers form at first a hollow sphere known as the blastula, whose wall consists of a single layer of cells. Some of these migrate into the hollow which they fill. The outer layer now represents ectoderm and the inner mass endoderm. The cells of the ectoderm become smaller than those of the endoderm and lose their yolk granules. A thick, spiny covering of a horny substance is now secreted by the ectoderm, and the round, prickly body thus formed falls away from the parent and rests for several weeks, during which it may be carried about by currents, in mud on the feet of water animals, etc. After a time the ectoderm differentiates into musculo-epithelial and interstitial cells, the mesogloea is secreted, the shell

cracks, and the embryo projects. A split in the endoderm forms the enteron, tentacles grow out, a mouth is formed, and finally the young hydra frees itself from the remains of the shell, moves away, and begins to feed and grow.

Asexual reproduction also begins with the formation of a swelling of ectoderm by the multiplication of the interstitial cells, which afterwards become converted into musculo-epithelial and endoderm cells, passing through the structureless lamella in the latter case. The result of this is an increase in the extent of the ectoderm and endoderm which leads to a bulging of the body wall. The knob or bud thus formed becomes larger, about four or five tentacles grow out around its free end, a mouth is formed, and finally the base narrows. Then the bud's tentacles attach themselves to a solid object, and pull the young creature apart from its parent. It grows in size and adds a few more tentacles. The buds arise in the middle or lower part of the body of the parent. Several may be formed at the same time, and a bud may form secondary buds before it is set free. While it is still on the parent, the bud is wholly a part of the body of the latter. Each of the layers of the parent is continuous with the corresponding layer of the bud, a suitable stimulus is transmitted by the nervous system from one to the other, and the entera are in free communication, so that food obtained by either is available for the other. In spite of this, bud and parent may attempt to swallow the same prey, while the parent may snatch food away from the young. In starved individuals buds may be withdrawn. Occasionally a hydra will reproduce by fission, the whole body dividing, either lengthwise or transversely, into two. In this event, as in the fission of *Paramecium*, structural development as well as the growth of each product of fission must take place after separation, whereas in the bud, as we have seen, the structural development takes place before fission.

REGENERATION

A property akin to asexual reproduction is that of regeneration or the replacement of lost parts, which is possessed by *Hydra* in a very high degree. To some extent all organisms have this power, but as a rule the higher the animal the less is its faculty for regeneration. In man it is little more than the power of healing wounds. Not only will *Hydra* grow anew any part, such as a tentacle, which is cut off, but any fragment of the body, provided

it be not too small and contain portions of both layers, will grow into an entire animal. This ability is connected with the presence of large numbers of the unspecialized interstitial cells.

OBELIA

HYDROID COLONIES

We must now look at the budding of *Hydra* from a somewhat different point of view. By the outgrowth of buds, the animal increases the size of its body in precisely the same way as *Carchesium*; that is to say, by the addition of new members, each of which repeats the whole structure of the body as it existed at first. In *Hydra* the process is carried further by the fission of the repeated part from the parent body, so that an act of reproduction takes place, but it is easy to imagine that this might not happen. The result would be the permanent conversion of the body of the *Hydra* into a colony, of which the buds would be the zooids. Now there are a number of animals related to *Hydra* in which this actually takes place. Such animals are known as hydroids, and nearly all of them are marine. A common example

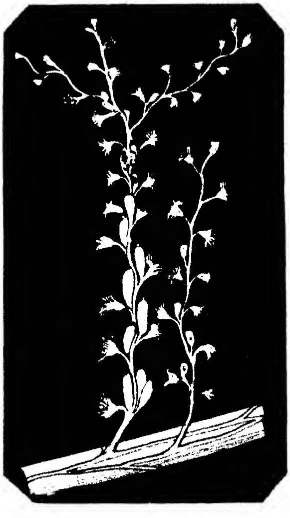


FIG. 9.11.—Part of a colony of *Obelia* seen under a hand lens.

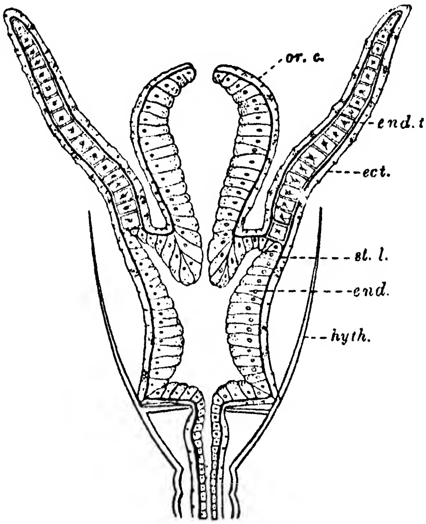


FIG. 9.12.—A longitudinal section of a hydranth of *Obelia*, highly magnified.

ect., Ectoderm; *end.*, endoderm; *end.t.*, endoderm of the tentacles; *hyth.*, hydrotheca; *or.c.*, oral cone *st.l.*, structureless lamella.

is *Obelia geniculata*, which is found growing upon seaweeds near low watermark on the British coast (Fig. 9.11).

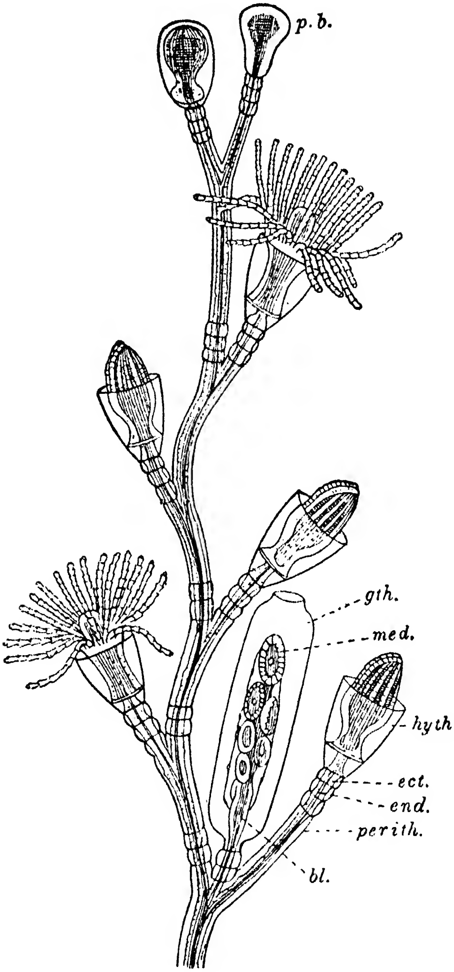


FIG. 9.13.—Part of a colony of *Obelia*, magnified.

bl. Blastostyle ; *ect.*, ectoderm ; *end.*, endoderm ; *gth.*, gonotheca ; *hyth.*, hydrotheca; *med.*, medusa bud ; *p.b.*, polyp bud ; *perith.*, perisarc.

ANATOMY OF THE POLYP

Certain comparatively unimportant differences distinguish the polyps of *Obelia* from those of *Hydra*. The tentacles are more numerous and, instead of being hollow, have a solid core of large endoderm cells, with very stout walls of intercellular substance

and highly vacuolated contents. In the ectoderm the muscular fibres are independent cells with nuclei of their own, lying below the epithelium. The oral cone is very large and forms a chamber above the rest of the enteron. From the middle of the basal disc of each polyp the body-wall is continued as a narrow tube, which joins the tubes from other polyps so as to form a branching structure like the body of a flowering plant (Figs. 9.12, 9.13). This is continuous at its base with a root-like arrangement of tubes known as the hydrorhiza, on the surface of the seaweed. The tubes of the whole structure are known as the cœnosarc, and the polyp heads as hydranths. The whole colony is enclosed in a perisarc of chitin (p. 157), which is secreted by the ectoderm and follows closely the outline of the body, but is separated from it by a small space, bridged by processes from some of the ectoderm cells. At the base of each hydranth the perisarc expands into a cup or hydrotheca into which the hydranth can be withdrawn.

THE MEDUSA

The generative organs are not borne by the polyps, but by special bodies, which originate as members of the colony, are set free by breaking away as the buds of *Hydra* are, and carry

FIG. 9.14.—A medusa of *Obelia*, magnified.

out sexual reproduction as independent individuals. These differ widely from the polyps, and are, indeed, so unlike them that their origin from the colony would never have been guessed unless it had been seen to take place, but they are fundamentally similar in structure (see p. 108). They are small jelly-fish or medusæ (Figs. 9.14, 9.15). Each has the shape of a mushroom with a short, thick stalk and a fringe of tentacles around the edge. The convex upper side is called the exumbrella, the concave lower side the subumbrella, the whole disc-shaped upper part the umbrella, and the stalk the manubrium. Around the edge of the subumbrella a low

ridge projects inwards. This is the velum and represents a much larger structure in the same region of many other medusæ. At the end of the manubrium is the mouth, which leads by a tubular gullet along the manubrium to a stomach in the middle of the body. From this four radial canals run outwards to a ring canal at the edge of the umbrella. The lining of all these internal spaces consists of endoderm, and the radial canals lie in a sheet of endoderm, known as the endoderm lamella. In fact we may regard the internal cavities of a medusa as corresponding to the enteron of a polyp in which the walls have come together over a large area, leaving certain spaces which form the gullet, stomach, and canals. The whole outside of the body and tentacles is covered with ectoderm. Between the ectoderm and the endoderm is a layer of jelly, which is very thick, especially on the exumbrella side. The medusa may be compared to a polyp which is greatly widened and shortened, the walls of the wide, flat enteron coming together in places, as we have seen, and the structureless lamella increasing in thickness to form the jelly. The manubrium represents the oral cone and the tentacles stand around it at a greater distance owing to the widening of the body. The arrangement of the organs of a medusa is an excellent example of what is known as radial symmetry. In bilateral symmetry (p. 187) the parts of the body are arranged on each side (right and left) of a plane, in such a way that no other plane will divide the body into two halves which are alike. In radial symmetry the parts of the body are arranged about a point in such a way that many planes divide the body into like halves. Polyps also are radially symmetrical.

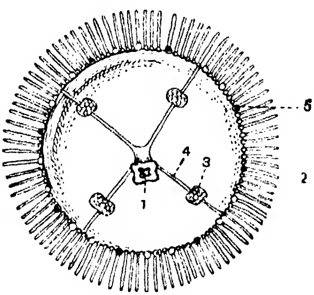


FIG. 9.15. — The medusa of *Obelia*, seen from the subumbrella side.—From Shipley and MacBride.

1, Mouth, at end of manubrium; 2, tentacle; 3, gonad; 4, radial canal; 5, statocyst.

MOVEMENTS OF THE MEDUSA

The medusa floats in the sea with the manubrium downwards and the tentacles hanging like the snaky locks of its classical namesake. It swims by contractions of the plentiful musculature of the subumbrella side, which drive water out of the umbrella and send the animal in the opposite direction. The contractions

are started by impulses which originate in the nerve net at the umbrella margin. There nervous transmission is facilitated by the nerve-rings—two specially well-developed circular tracts of the net—and there is provision for keeping balance by means of eight sense organs, known as statocysts, situated each at the base of one of the tentacles. These are small hollow vesicles each containing a calcareous body which hangs in a single cell that secreted it. The swaying of the calcareous bodies against fine

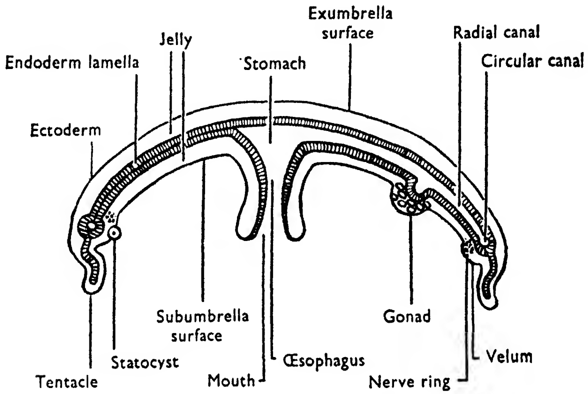


FIG. 9.16.—Medusa of *Obelia*. A diagram of a vertical section, passing through a radial canal on one side and a statocyst on the other ; these are not on the same diameter

processes on sense-cells which line the outer side of the vesicle gives rise to impulses by which the movements of the animal are regulated through the nervous system, stronger contractions being caused on the side which is at the lower level.

REPRODUCTION

Each medusa is of one sex only. The generative organs, which are not fully developed till after the animal is set free, are four in number and lie on the subumbrella below the radial canals. Each consists of a knob of ectoderm, into which passes a short branch from the radial canal. The germ-mother-cells originate in the ectoderm of the manubrium, migrate into the endoderm, and pass along the radial canals to the generative organs, where they migrate into the ectoderm again. When the ova or sperms are ripe, they are shed by the rupture of the ectoderm into the water,

where fertilisation takes place. Development similar to that of *Hydra* leads to a free-swimming stage called a planula, with solid endoderm and ciliated ectoderm (Fig. 9.16). It then settles down by its broader end, an enteron is formed by a split in the endoderm, tentacles and a mouth form at the other end, and thus there develops a polyp, from which a colony arises by budding. When the colony has reached a certain size there appear, in the angles between the stem and the branches which bear the hydranths, tubular outgrowths known as blastostyles, each enclosed in a vase of perisarc known as a gonotheca. A blastostyle and its gonotheca

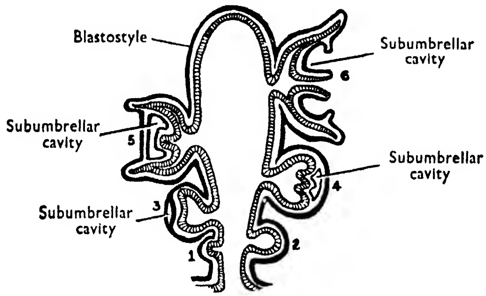


FIG. 9.17.—A diagram of the development of medusæ. 1–6, stages in the development of buds on the blastostyle.

are together known as a gonangium. The blastostyle is probably an incomplete zooid. On its sides are formed a number of buds which develop into little medusæ and escape through the opening at the top of the gonotheca (Fig. 9.17).

ALTERNATION OF GENERATIONS

It will be seen that *Obelia*, like *Hydra*, reproduces itself both sexually and asexually. Sexual reproduction is carried out by the medusa and leads to the formation of polyps. The asexual reproduction consists in the budding off of medusæ from the polyp stock. But whereas in *Hydra*, the two processes go on side by side, sometimes in the same individual, and succeed one another quite irregularly, in *Obelia* there are two different types of individual—the polyp stock and the medusa—which follow one another regularly and are each confined to one method of reproduction. Thus we have a definite alternation of generations, a sexual and an asexual form succeeding one another. It will be remembered that such generations also alternate in *Monocystis* and

that the malarial parasite has a more complicated life-history of the same kind. The asexual generation of *Obelia* is relatively inactive, gathering much nourishment and spending little: the sexual generation is active, spending its substance freely in locomotion, which ensures the distribution of the species and thus opens up fresh food supplies and increases the chances of escape from local dangers. The gist of the story is the distribution of labour among individuals of different kinds.

METAGENESIS

The designation 'alternation of generations' has been applied to a number of different types of life-history which have in common only the fact that reproduction is accomplished differently in successive phases of the reproducing organism. It is a useful 'omnibus' term but should not be taken to imply more than superficial resemblance between the processes it covers. The type met with in hydroids is known as metagenesis. We shall observe a quite different process, which does not involve asexual reproduction, in the liver fluke and again in a nematode worm. Botanists restrict the term to life-histories, such as those of mosses and ferns, where a stage with only a single set of chromosomes (p 702) alternates with one containing a double set. This condition is found in animals only in the Sporozoa. In view of this diversity of usage, many biologists prefer not to speak of the life-history of *Obelia* as an alternation of generations, but to use for it the term metagenesis.

REPRODUCTION AND COLONY-BUILDING

The above account of the reproduction of hydroids differs in one respect from that which is sometimes given. On the analogy of the budding of *Hydra*, some authors regard the formation of a hydroid colony by budding as a kind of asexual reproduction in which there are formed numerous 'individuals' which do not separate. If that is so the alternation of generations contains an indefinite number of acts of asexual reproduction between two sexual acts. We have preferred to treat the polyp stock as one individual containing a number of semi-independent parts—the hydranths—each of which repeats the structure of the whole body as it was at first, and having certain other parts—the blastostyles and most of the cœnosarc—which are differently constructed, serve the entire body, and are wholly dependent

upon it. This view involves the following considerations. The development of the individual and its reproduction are essentially the same process—morphogenesis, which is also at work in regeneration. Any part of an organism, from the smallest organ to the whole body, is liable to be repeated, with or without differences between the repeated parts. This phenomenon has been called merism : we have seen it in cilia, trichocysts, contractile vacuoles, cells, limbs, zooids, etc. Sometimes, as in cilia, cells, or zooids of the same kind, it has not involved differences. Sometimes, as in cells or limbs or zooids of different kinds, it has involved differences between the repeated parts. Sometimes the parts are present in their full number from the first ; sometimes they increase in number as growth goes on. From time to time every organism produces a part which not only repeats its whole structure, but also separates from it by an act of fission. This process is reproduction. In some types of reproduction, as in the budding of *Hydra*, the repetition of structure takes place before separation. In others, as in the formation of germ cells,[1] the part which separates is simple in structure, but has the power of repeating the structure of the parent body after fission.

INDIVIDUALITY

The term individual, whose application was in question in the foregoing paragraph, has been used in zoology with very different meanings, which are well illustrated by the life-history of the hydroids. An individual is a single complete living being. Since the medusa carries out all the functions of life in itself, it seems natural to assert that it is a complete living being, and since, as we have seen, its structure is essentially that of a polyp, we might assume that each polyp is also an individual. On the other hand, the whole polyp stock is a unit, and we might consider it to be one individual, of which the separate polyps are members, still regarding the medusa as an individual. Of these alternatives the first is open to the objection that it ignores the fact that the stock with all its polyps may be regarded as a whole since it has common nourishment and reproductive organs (the gonangia), and obliges us to regard as individuals the blastostyles, which are morphologically equivalent only to parts

[1] Here there may be the additional complication that two such separated parts so develop as to produce but one body after fusion.

of other individuals. The second alternative is that which we have adopted above. It may be stated as follows : 'Every continuous mass of living matter which arises normally by fission is an individual'. That view has the advantage that it does not force us to create artificial units of any kind. According to it, the act which makes an individual is the act of fission by which it becomes independent of its parent, and fertilisation is the blending of two undeveloped individuals into one, while the polyp stock is an individual which contains a number of units meristically repeated, and the medusa is an individual consisting of one unit of the same type as those which exist in the polyp stock. All the products which one individual produces by fission, such as the medusæ of a single hydroid colony or the whole family produced by the repeated fission of a *Paramecium*, are collectively known as a clone.

CŒLENTERATA

The phylum Cœlenterata, to which *Hydra* and *Obelia* belong, differs from all other groups in that its members have a body-wall composed of two layers of cells only, the endoderm and ectoderm ; they are therefore called Diploblastica. The rest of the Metazoa, called collectively Triploblastica, not only have generally bulkier bodies many cells thick, but, after their embryos have reached a stage where the two layers of endoderm and ectoderm are present, they develop a third and usually detached layer between them ; it is called the mesoderm. In place of this the cœlenterates have the secreted jelly-like mesogloea, which has little or no structure, although cells sometimes wander into it. Other structural features of the group are the radial symmetry, the nerve-net, and the cavity or enteron in the endoderm with a single opening which serves as both mouth and anus. The first and second of these they share with the echinoderms, in the third they resemble the flatworms. Except for *Hydra* and a few other aberrant genera, all cœlenterates are marine.

SUBPHYLUM I—CNIDARIA

Most of the cœlenterates, including both *Hydra* and *Obelia*, belong to this group. They move by muscle-cells, and possess nematocysts. The body is organised on a plan which can be

reduced either to a polyp or to a medusa, and often the two forms alternate in one life-history. There is, in fact, little difference, except in shape, between the two, as can be shown by drawing a polyp in section upside down alongside a similar drawing of a medusa (Fig. 9.18). The larva is typically a planula. There are three classes.

CLASS I—HYDROZOA

There is generally an alternation of polyp and medusa, the former being colonial; the tentacles of the polyp are usually

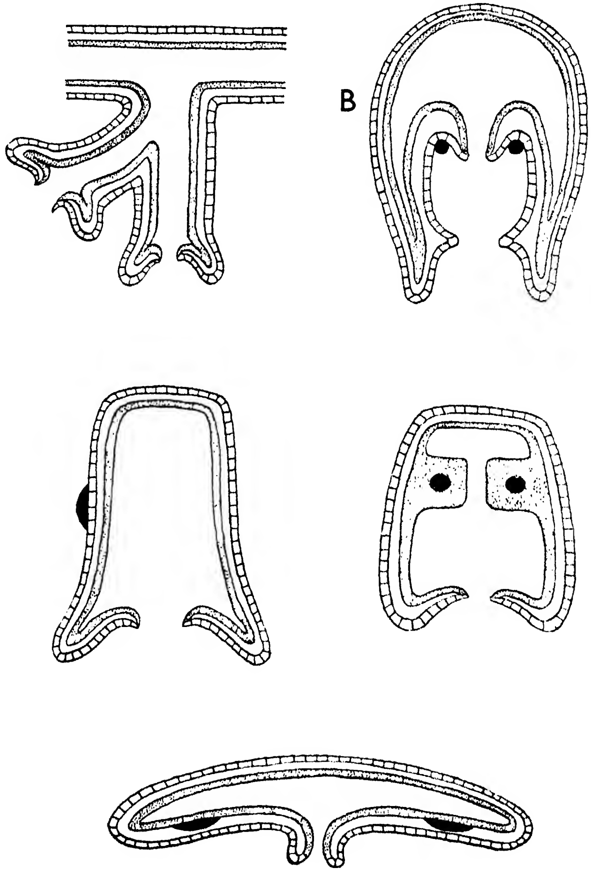


FIG. 9.18.—Diagrammatic vertical sections of polyps and medusæ. All are shown with the mouth below, whatever the natural position. Endoderm dotted; ectoderm hatched; gonads in solid black.

A, Hydrozoan polyp; *B*, hydrozoan medusa; *C*, hydridan polyp; *D*, actinozoan polyp; *E*, scyphozoan medusa.

solid; there are no vertical partitions in the enteron; the medusa has a velum and a nerve ring; the gonads are formed in the ectoderm; and there is usually an external skeleton. *Obelia* is a typical member of the class. In some genera, especially those living in the tidal zone (e.g. *Tubularia*), the medusa remains attached to the polyp and the egg develops *in situ* into a peculiar creeping larva, the actinula. In still other genera the medusa is completely suppressed, and *Hydra* may be looked on as an extreme example of such suppression, having also other peculiarities, such as the hollow tentacles and solitary habit. In some orders, on the other hand, the polyp has disappeared. In the order Siphonophora, including *Physalia*, the Portuguese man-of-war, the colonies float freely on the surface of the sea, and the polyps are of many different forms with specialised functions.

CLASS II—SCYPHOMEDUSÆ

The medusa is the predominant phase, but there is also a polyp which forms the medusæ by transverse fission. The tentacles are solid, but otherwise the characters are the opposite of those of the Hydrozoa, that is to say, the enteron has vertical partitions; there is no velum or nerve ring; the gonads are formed in the endoderm; and there is no skeleton. Beneath the gonads are sub-genital pits in the ectoderm of the subumbrella.

A typical member is the common jellyfish, *Aurelia aurita*, shown in Fig. 9.19 and in section in Fig. 9.20. From the main digestive cavity a series of radial canals, some branched, run out to a circular canal running round the edge of the disc. Through these a circulation of sea water is kept up by cilia, the stream going out by the eight unbranched canals and returning by the alternating branched ones. Partially digested particles of food are carried in the stream, and are ingested by any endodermal cell which needs them. Possibly also the current helps in taking oxygen to the cells, for many jellyfish are of large size (*Cyanea aurita* may be six feet in diameter) and considerable thickness. The bulk of the body is, however, mesogloea. The eggs are liberated into the enteron, are fertilised there, and develop into planulæ. These escape, and settle on a rock or weed, and each develops into a polyp known as a scyphistoma. This may divide by budding into more polyps like itself, but its chief function is to produce

medusæ by a series of horizontal fissions, the whole process being called strobilisation (Fig. 9.21). The structure looks much like a

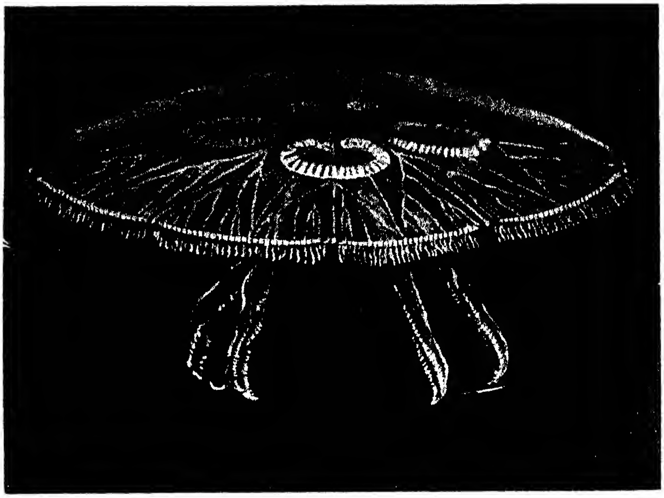


FIG. 9.19.—A small specimen of the common jellyfish, *Aurelia aurita*, natural size.

Note the horseshoe-shaped gonads, showing through the transparent tissues ; the radial canals, alternately branched and unbranched ; the little sense tentacles in notches each opposite the middle branch of a canal ; the marginal tentacles ; and the arms of the manubrium, each folded and fringed.

Water circulates from the stomach by the unbranched (adradial) canals to the circular canal, and back by the branched (per- and inter-radial) canals.

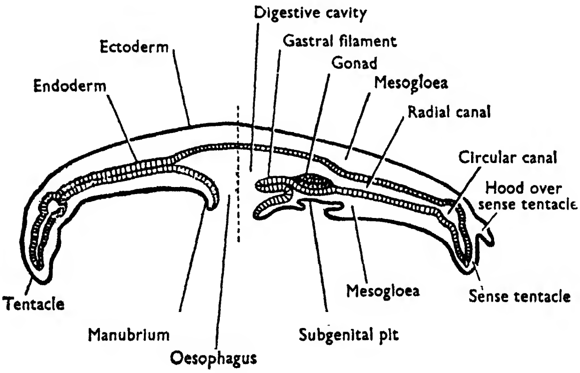


FIG. 9.20.—*Aurelia*. A diagram of a vertical section, passing through a radial canal on one side, and a tentacle on the other ; these are not on the same diameter. The dotted line divides the section into two halves.

pile of saucers, of which each in turn, known as an ephyra, as it becomes the top one floats off, turns over, and grows to be a new jellyfish. Strobilisation occurs only in winter and when the

animal is well fed. There is much variation in the development of the species of this class, and even in individuals of a species. Some genera, including *Haliclystus* and *Lucernaria* of British coasts, have only one stage in the life-history, which is a sessile polyp.

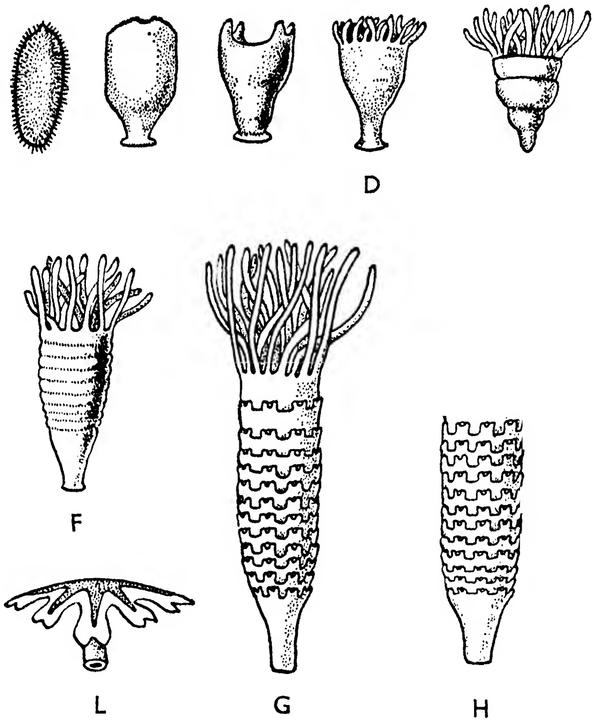


FIG. 9.21.—The life-history of *Aurelia*.

A, Planula; *B-H*, stages in the development of the scyphistoma; *L*, ephyra.

CLASS III—ACTINOZOA

A medusa is never present; the tentacles are hollow; the enteron has vertical partitions (mesenteries); the gonads are formed from the endoderm; and there may or may not be a skeleton.

The typical members of this class are the sea-anemones, illustrated in Figs. 9.22, 9.23. These are solitary forms, usually capable of many muscular movements both of feeding and

locomotion. They have a ciliated ectoderm, and in the plankton feeders, such as *Metridium*, this is important in carrying food to the mouth. Others, such as the common *Actinia equina*, kill and eat relatively large animals which accidentally touch the tentacles, and experimentally can swallow pieces of flesh almost as large as themselves. The larva is a planula, which develops

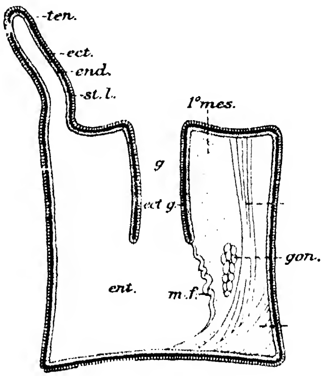


FIG. 9.23.—A diagram of a vertical section of a sea-anemone.

ect., ectoderm of tentacle ; *ect.g.*, ectoderm lining gullet ; *end.*, endoderm ; *ent.*, enteron ; *g.*, gullet ; *gon.*, gonad ; *m.f.* mesenterial filament ; *mus.*, longitudinal or 'retractor' muscle ; *mus'*. oblique or 'parietal' muscle ; *st.l.*, mesoglœa ; *ten.*, tentacle; 1°*mes.*, primary mesentery.

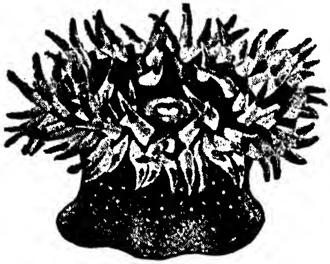
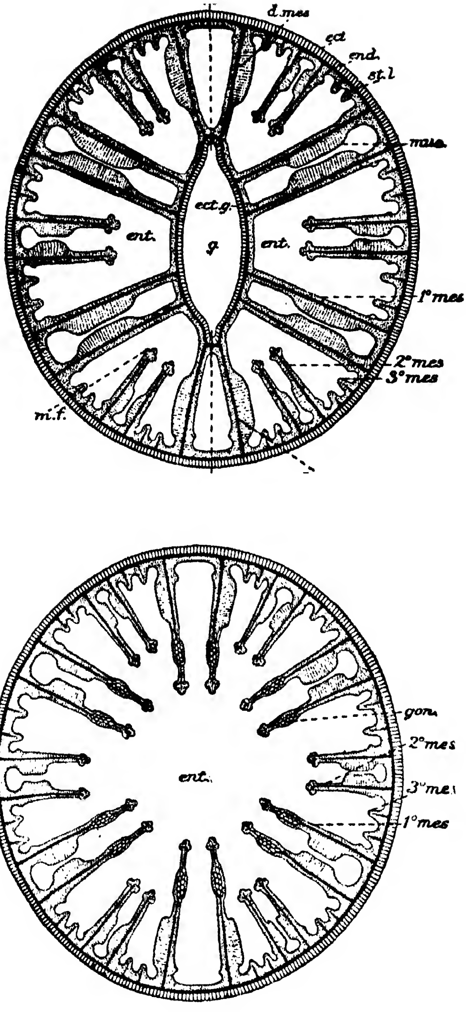


FIG. 9.22.—External appearance of *Tealia felina*, a sea-anemone. —From Thomson.

directly into a new polyp. Many Actinozoa are colonial, and amongst such forms are most of the corals. These include the red coral, which forms its calcareous skeleton in the mesogloea, and the reef-building species in which it is external. The coral reef, which may be thousands of feet thick, consists of a large mass of calcium carbonate built up by past generations of animals. The living individuals protrude from tubes of this material only in the narrow zone from the surface to a depth of twenty or thirty fathoms. Many corals contain symbiotic yellow dinoflagellates known as zooxanthellæ, comparable to the green bodies of *Chlorohydra*.

SUBPHYLUM II—CTENOPHORA

These differ from other cœlenterates in having neither polyp nor medusa, in being without nematocysts, and in swimming by cilia instead of by muscular cells. Some zoologists would raise them to a separate phylum. They are all marine, and are known



B

FIG. 9.24.—Diagrams of transverse sections of a sea-anemone.

A., Through the gullet; *B*, below the gullet.

d.mes., 'directive' mesentery; *ect.* ectoderm; *ect.g.*, ectoderm of gullet; *end.*, endoderm; *ent.*, enteron; *gon.*, gonad; *g.*, gullet; *m.f.*, mesenterial filament; *mus.*, muscle; *spg.*, siphonoglyphs; *st.l.*, mesogloea; 1°*mes.*, 2°*mes.*, 3°*mes.*, primary, secondary, and tertiary mesenteries.

as sea-gooseberries, a name which roughly describes their appearance. The cilia are arranged in eight conspicuous rows, and there

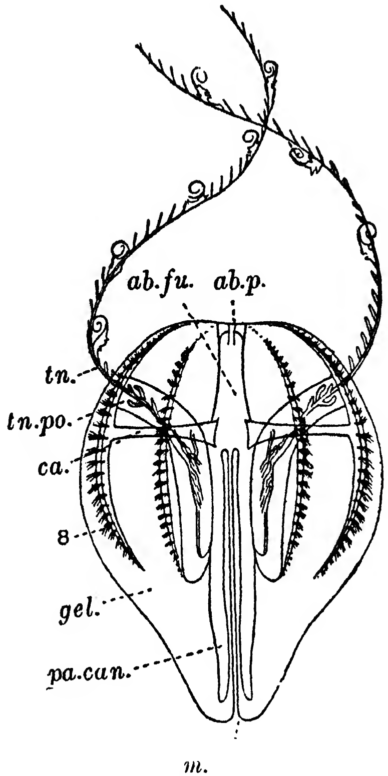


FIG. 9.25.—*Hormiphora plumosa.* × *c.* 6.—From Borradaile and Potts, *The Invertebrata*, 2nd edition, 1935. Cambridge University Press. After Chun.

ab.p., aboval pole; *ab.fu.*, aboval funnel; *tn.*, tentacle; *tn.po.*, tentacular pouch; *ca.* and 8, one of the rows of cilia; *gel.*, gelatinous material; *pa.can.*, paragastric canal; *m.*, mouth.

may be two long tentacles. *Hormiphora plumosa* (Fig. 9.25) is a common British form.

10

FLATWORMS

MANY of the lower animals are popularly known as 'worms'. They have little in common save that their bodies are longer than they are broad and have bilateral symmetry, and that their organisation is rather simple. The lowliest of such creatures are known as the flatworms or Platyhelminthes.

FASCIOLA

An example of these is the liver fluke, *Fasciola hepatica* (=*Distomum hepaticum*), which is often found in the bile ducts of sheep kept in damp meadows, causing a serious and usually fatal disease known as 'liver rot', in which the wool falls off, dropsical swellings appear, and the animal wastes away. It is occasionally found in cattle, and more rarely a wide variety of mammals from kangaroos to man. It is a flat, brownish worm (Fig. 10.1), about one inch long by half an inch broad, shaped like a leaf with a blunt triangular projection at the broader end. At the tip of this projection lies the mouth, in the midst of an anterior sucker, and just behind the projection an imperforate posterior or ventral sucker is placed in the middle of the ventral side; when the worm is kept in the laboratory it moves by looping, with alternate attachments of the suckers. Nearly midway between the suckers is a smaller genital opening, at the hind end of the body is a minute excretory pore, and on the dorsal surface at about a third of the length of the animal from the front end lies the opening of the Laurer-Stieda canal presently to be mentioned. The body is covered witha cuticle, in which little backward-pointing spinules are embedded.

GUT

The mouth leads into an ovoid, muscular pharynx, from which a short œsophagus passes backwards to divide before the posterior sucker into right and left branches or intestines, which

run on either side of the middle line to the hind end of the body, giving off on either side many offsets, which in turn are much branched There is no anus The worm feeds largely on the blood of its host, which is sucked from the wall of the duct, but probably also on pieces of tissue rasped off by the sucker It can also absorb sugars, especially monosaccharides such as glucose and fructose, through the general body surface.

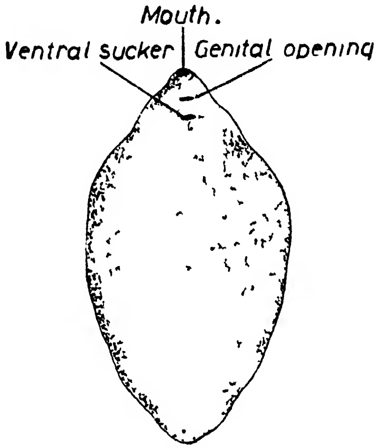


FIG. 10.1 The liver fluke

LAYERS OF THE BODY

The ectoderm cells have sunk inward after secreting the cuticle Below the cuticle lie successively circular, longitudinal, and diagonal layers of muscle fibres, with the epidermal cells among the longitudinal fibres (Fig. 10.2). Between these and the endoderm, which is a columnar epithelium lining the gut, lies the parenchyma, a meshwork of protoplasm with nuclei at the nodes and oval cells in the meshes. Muscle fibres pass across the parenchyma from the dorsal to the ventral side of the body. There are no blood vessels or cœlom. It will be noticed that in the fluke a mass of tissue lies between the ectoderm and endoderm in place of the structureless lamella of *Hydra*. This is known as the mesoderm. We shall allude to it in more detail in describing the earthworm.

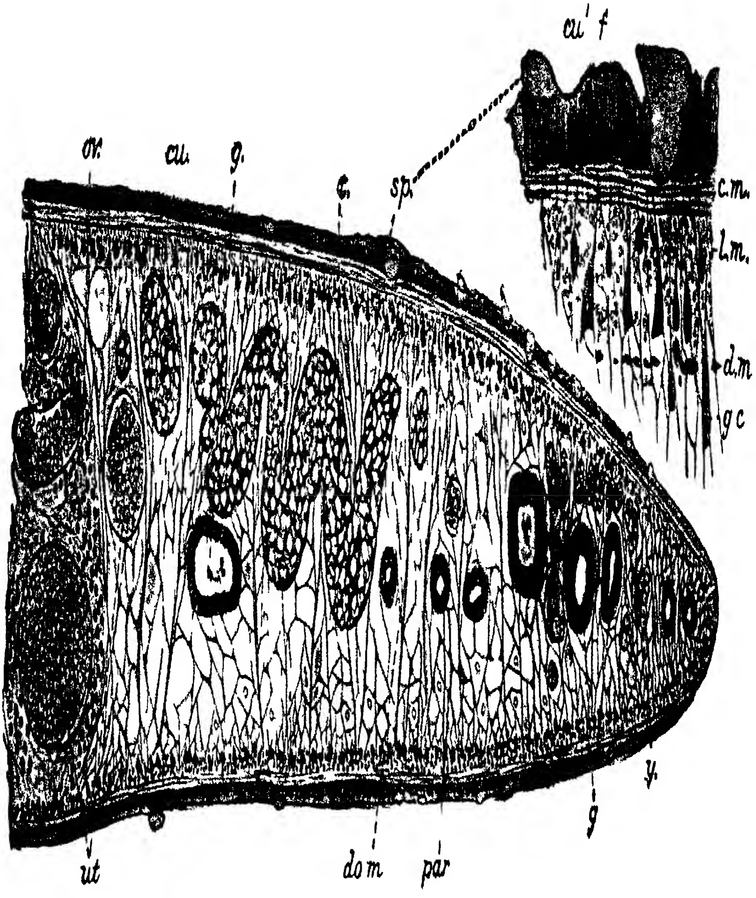


FIG. 102.—A transverse section of a liver fluke, with a portion more highly magnified

c m Circular muscle layer *cu* cuticle *cu'* unfibrillated surface layer of the same *d m* diagonal muscles *do m* dorsoventral muscle strands *g* gut *f* vertically fibrillated layer of the cuticle *g c* gland cells of the skin *l m* longitudinal muscle layer *ov* ovary *par* parenchyma *sp* spindle cut transversely at various levels *t* testis *ut* uterus containing eggs *y* yolk gland

RESPIRATION

There is no evidence that the liver fluke is anaerobic (p. 11). Experimentally a reduced oxygen tension shortens the life of the worms, and measurements show that bile is nearly saturated with oxygen.

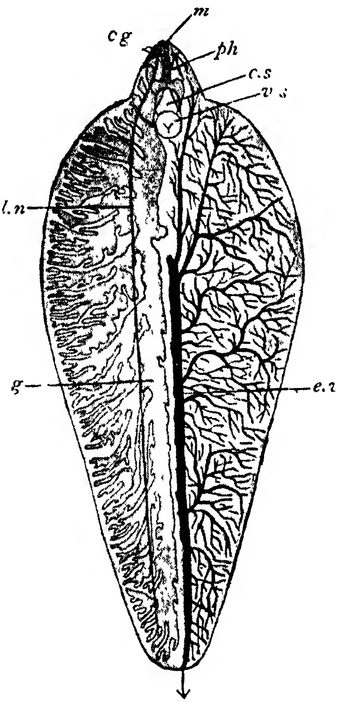


FIG. 10.3 — The structure of a liver fluke. – After Sommer From the ventral surface. The branched gut (*g*) and the lateral nerve (*l.n.*) are shown to the left of the figure, the branches of the excretory vessel (*e v.*) to the right.

c.s., Position of cirrus sac; *cg.*, lateral head ganglion; *m.*, mouth; *ph*, pharynx; *v.s.*, ventral sucker. An arrow indicates the excretory aperture.

EXCRETORY SYSTEM

The excretory system (Fig. 10.3) lies in the parenchyma. It consists of a meshwork of tubules joining into a main duct which lies in the middle line, from a point about a quarter of the length of the body behind its front end to the excretory pore at the hind end. The ultimate branches of the tubules are very fine and end, at least in the larva, in little structures known as flame cells or solenocytes (Fig. 10.4). These are minute vesicles containing a few long cilia which keep up a flickering movement like that of a flame and so perhaps drive towards the main duct the fluid secreted into the vesicle by its walls. Each vesicle has a nucleus and may be regarded as a hollow cell. It is connected with its fellows by fine protoplasmic processes which are said to be hollow. The flame cells are said to disappear in the cercaria stage (p. 123) and to be invisible in the adult. The whole system is derived from the ectoderm and is called a protonephridium.

The fluid in the tubules contains much fat, and is almost continuously squeezed out through the excretory pore by contractions of the body. Fat is an unusual excretory product, but

its occurrence is perhaps connected with the nature of the food; it is present also in the urine of the highly carnivorous and largely blood-feeding cats. The chief nitrogenous product is ammonia.

NERVOUS SYSTEM

The nervous system includes a brain which consists of a collar around the pharynx with a mid-ventral swelling and a pair of lateral swellings. From these swellings or ganglia nerves are given off to the forepart of the body, and from each lateral ganglion arises a large lateral nerve cord which runs backwards below the gut to the hinder end of the body, giving off branches on the way. The nerve cords contain nerve cells as well as fibres.

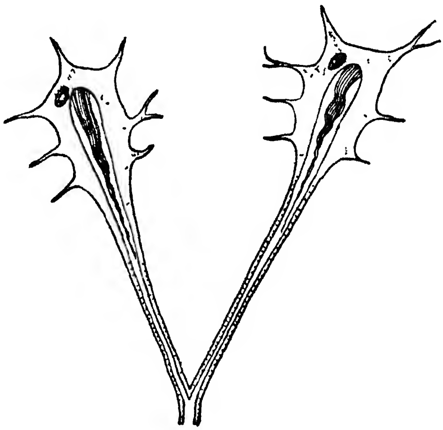


FIG 10 4.—Two flame cells, highly magnified

GENERATIVE ORGANS

The liver fluke is hermaphrodite, and has very complex generative organs (Fig. 10.5). The testes are two much-branched tubes lying one behind the other in the middle part of the body. The branches of each are gathered into a vas deferens, and the two vasa deferentia run forwards side by side to join, above the posterior sucker, a large, pear-shaped seminal vesicle. From this a fine, somewhat twisted tube, the ejaculatory duct, passes forwards to enter a stout, muscular penis or cirrus, which opens at the generative pore. Normally the penis lies in a cirrus sac, but it can be turned inside out and thus thrust out of the pore. The ovary is a branched tubular structure on the right side in front of the testes. Its branches join to form the oviduct, which passes towards the middle line and there joins the yolk duct. This is formed by the union of two transverse ducts, which lead each from a longitudinal duct at the side of the body. The yolk glands are very numerous, small, round vesicles lying along the

sides of the body, and communicating by short ducts with the longitudinal ducts. The Laurer-Stieda canal is a short tube leading from the union of oviduct and yolk duct to a pore on the back; it is probably functionless, but in other species it serves for copulation. The oviduct and yolk duct are surrounded where

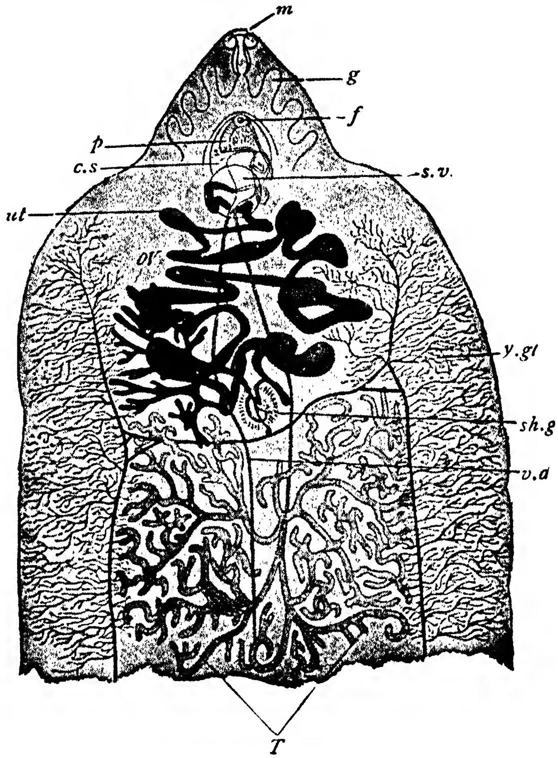


FIG. 10.5.—The reproductive organs of a liver fluke, from the ventral side.—After Sommer.

c.s., Cirrus sac; *f.*, female aperture; *g.*, anterior lobes of gut; *m.*, mouth; *ov.*, ovary (dark); *p.*, penis; *s.v.*, seminal vesicle; *sh.g.*, shell gland; *T.*, testes (anterior); *ut.*, uterus; *v.d.*, vas deferens; *y.gl.*, diffuse yolk glands.

they join by a rounded mass, which is known as the shell gland; according to some authors it forms the egg shell, but others say that this is made by the yolk glands, which are numerous, minute, and unicellular. The shell glands may harden the shell, or their secretion may activate the sperms. From this point the joined ducts proceed forwards as a wide, twisted tube, the uterus, to

the generative opening. The uterus contains eggs, each enclosed in a shell, within which lie, besides the ovum, a number of yolk

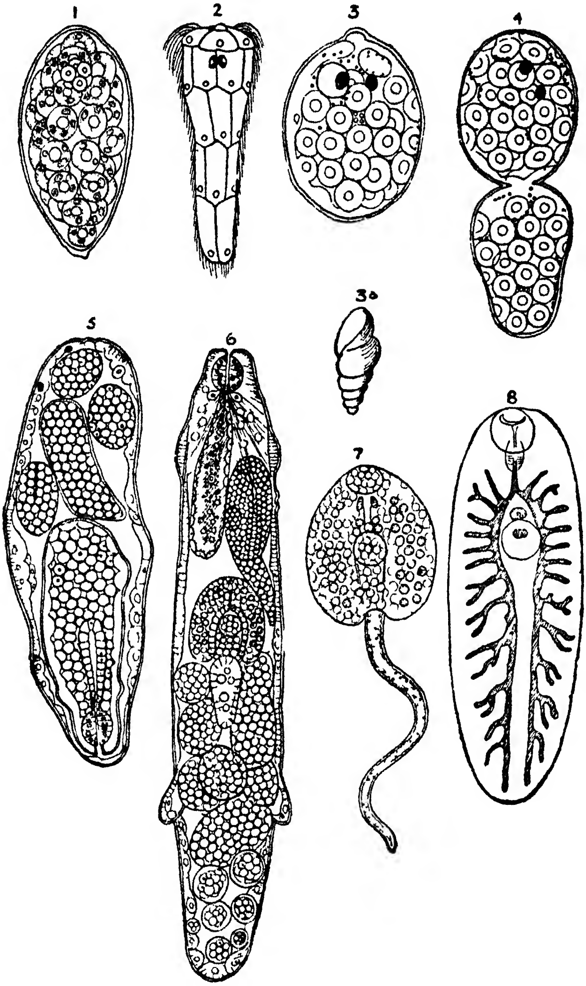


FIG. 10.6.—The life-history of a liver fluke.—After Thomas.

1. Developing embryo in egg-case ; 2. free-swimming ciliated embryo ; 3. sporocyst ; 3*a*. shell of *Limnæa truncatula* ; 4. division of sporocyst which sometimes occurs ; 5. sporocyst with rediæ forming within it ; 6. redia with cercariæ forming within it ; 7. tailed cercaria ; 8. young fluke.

cells derived from the yolk glands, and spermatozoa. The material of the shell is a quinone-tanned protein similar to the sclerotin of insects (p. 220). The animal is probably as a rule self-fertilised.

LIFE-HISTORY

The life-history of the liver fluke is a remarkable and interesting process (Fig. 10.6). The eggs, up to 3,500 a day, are laid in the bile ducts of the sheep. So long as they remain within the body of the latter they do not develop, but when they have been carried by the bile to the intestine, and thence passed to the exterior with the droppings, they will develop in damp spots if the weather be warm, and the pH of the water be less than 7.5, the optimum being about 6.5. In a few weeks a larva known as the miracidium emerges. It is rather more than a tenth of a millimetre long, conical, covered with a layer formed by five rings of big, ciliated cells, provided with two eye-spots, a small gut, and two flame cells, and filled by a mass of cells. It swims by means of the cilia, with the broad end forwards. At this end there is a knob which can be thrust out as a conical spike. If it can find a member of a particular species of water snail known as *Limnæa truncatula* [1] it butts this repeatedly until it becomes lightly attached, perhaps by suction ; there is then cytolysis of the surface of the snail, presumably enzymic, the fluke extends a papilla into the wound, and suddenly the whole larva passes into the snail, the whole process having taken about 30 minutes. There is no rotation, and, as the cilia are lost before the final penetration, the larva that enters is a new form called a sporocyst. This increases in size and sometimes multiplies by dividing transversely. Within the sporocyst some of the cells lining the cavity behave like fertilised ova, dividing to form a blastula, which invaginates to give rise to a two-layered sac or gastrula. These cells, however, have not undergone fertilisation, and their development is an example of parthenogenesis, the development of unfertilised ova. The gastrula grows into another form of larva, the redia, which bursts out of the sporocyst and migrates, usually into the liver of the snail. The rediæ devour the tissues of the snail and finally kill it. Each redia has an elongated body with an anterior mouth, a muscular pharynx, and a short, sac-like gut. A little way behind the pharynx the body-wall is thickened to form a muscular collar, and not far from the hind end are two blunt conical processes on one side. Posteriorly there is a large body cavity lined by an epithelium

[1] Other species and genera of water snail are sometimes infected in foreign countries, and occasionally *L. stagnalis* and others may be infected in Britain.

like that of the cavity in the sporocyst. Cells derived from the wall of the body cavity develop in much the same way as in the sporocyst and give rise to daughter rediæ, which escape from the parent by an opening behind the collar. Several generations of rediæ usually succeed one another, but eventually they cease to produce daughters of their own kind, and give birth instead to creatures known as cercariæ, with a flat, heart-shaped body, two suckers, a forked gut, and a tail. The cercaria, which is about 0.3 mm. long, with a tail of twice that length, emerges from the redia, works its way out of the snail, and swims by means of the tail. Soon it settles upon a wet blade of grass, loses its tail, secretes around itself a cyst by means of special cystogenous cells of the ectoderm, and waits till the grass is eaten by a sheep ; during this interval the larva, which is now known as a metacercaria, undergoes some slight structural

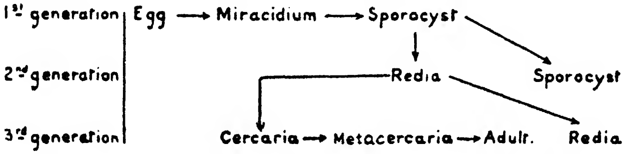


FIG. 10.7.—A diagram of the life-history of the liver fluke.

changes. The larva may remain alive inside the cyst for twelve months, but is killed by sunshine and drying. In the gut of the sheep the metacercaria is activated and escapes through a perforation in the cyst ; it then pierces the intestinal wall so that it enters the body cavity, and in two or three days bores into the liver. Later it enters the bile ducts and there grows into an adult fluke. When the gonads are fully developed, which is ten to twelve weeks after infection, the worms begin to lay their eggs, and migrate to the duodenum of the host. Flukes may live for eleven years, or may be lost with the fæces, and if the sheep survives till this happens it will usually recover, though, owing to permanent damage to the liver, the recovery is never complete.

It will be seen that in this life-history we have an example of alternation of generations far more complicated than that of *Obelia*, and differing from the latter also in that not sexual and truly asexual, but sexual and parthenogenetic generations succeed one another. The former kind of alternation of generations is known as metagenesis, the latter as heterogamy. It should also be noticed that there are three kinds of individual involved in the cycle.

The life-history of the liverfluke is shown by a diagram in Fig. 10.7.

The internally parasitic flukes usually have a life-history of the same general pattern, with the adult in a vertebrate and the larvæ in a mollusc, although there are variations in detail and some species do not have an intermediate host. Another important example is *Schistosoma* (=*Bilharzia*), an important parasite of man of which various species are found in Africa, Asia, and America. The adults live in the veins, and are peculiar in being diœcious. The female lives for most of the time in a groove, formed by the rolling up of the male (Fig. 10.8), but she can leave this and does so to lay her eggs in the capillaries. It is the eggs which cause the disease schistosomiasis by penetrating the walls of the capillaries with their spines and by secreting an enzyme and causing hæmorrhage. Eventually the eggs get into the bladder and leave the body in the urine. When this is diluted they hatch into miracidia which have a life of about thirty hours, during which they must infect a snail. Here two generations of sporocysts, and eventually cercariæ, are formed, but there are no rediæ. The cercariæ are set free, and can penetrate any part of the skin of man. In countries where the parasite is common, any contact with fresh water is therefore dangerous, as a mere splash may bring the cercariæ on to the skin. The parasite is very successful and in some areas is present in all the human population.

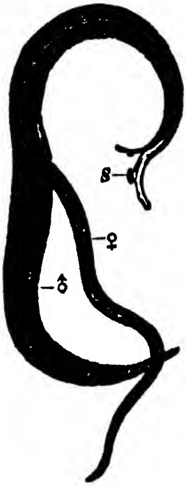


FIG. 10.8.—*Schistosoma hæmatobium*.—From Sedgwick.

♂, male; ♀, female; *S*, sucker

TÆNIA

Tænia solium (Fig. 10.9), found in man, is an example of another type of flatworm, the tapeworms. There is seldom more than one worm in the host (hence the trivial name) but it may reach a length of twenty feet. It lives in the intestine, in the wall of which the holdfast or scolex (or head, though some zoologists think it is morphologically posterior) is usually buried. On the scolex are four lateral suckers, and a crown of 22–32 hooks which

are borne in two rows on a projection or rostellum. Behind the scolex is a narrow neck, which is continually forming new sections of the body, called proglottides, of which there may be as many as 1,000. Each proglottis (there is no excuse for the illiterate

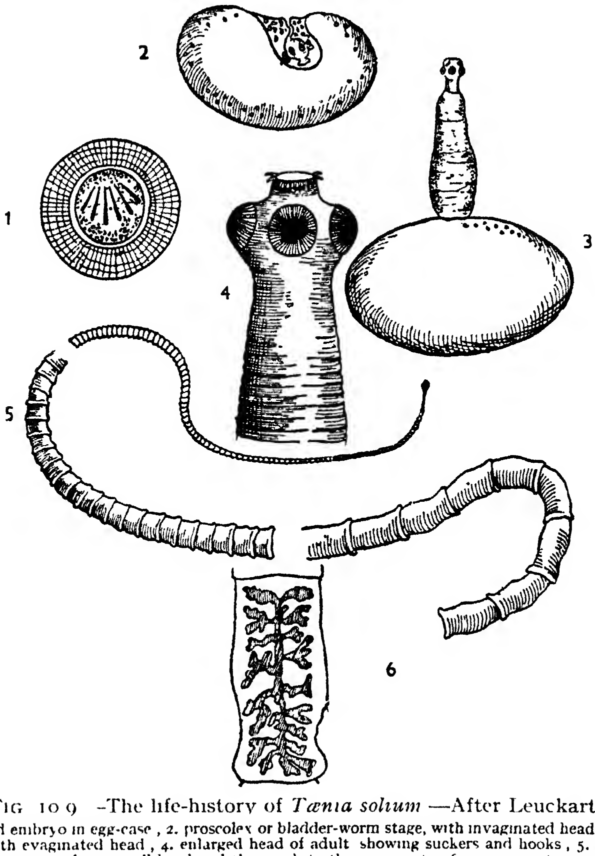


FIG. 10 9.—The life-history of *Tænia solium*.—After Leuckart.

1. Six hooked embryo in egg-case, 2. proscolex or bladder-worm stage, with invaginated head, 3. bladder-worm with evaginated head, 4. enlarged head of adult showing suckers and hooks, 5. general view of the tapeworm, from small head and thin neck to the ripe joints, 6. a ripe joint or proglottis with branched uterus, all other organs are now lost

form, proglottid) is pushed away from the neck as the next is formed, so that a chain is produced with the youngest links most anterior. Such a chain is called a strobila. The proglottides thus differ in their formation and arrangement from the segments of annelids, arthropods or chordates. When a proglottis is formed it possesses nervous tissue and execretory canals continuous with those of the head ; as it grows older it becomes larger, and reproductive organs develop in it. Young proglottides are broader

than they are long, but these proportions are reversed in those which are sexually mature.

The body is covered with a non-cellular cuticle, under which lies a layer of circular muscle fibres and then one of longitudinal muscle fibres. Next come two layers that are difficult to interpret, but which include some cells with radial fibres. Inside these is a mass of parenchyma like that of the fluke, in which are embedded the other systems. There is no alimentary canal. There is a flame-cell system of the same type as that of the fluke, with a large transverse duct on each side, connected by a transverse vessel on the hinder side of each proglottis and by a ring in the holdfast. Liquid passes backwards in the main duct, and in the last proglottis the vessel opens by a median pore. The nervous system consists of a transverse commissure and two rings in the holdfast, small forward nerves, two lateral nerve cords, and branches.

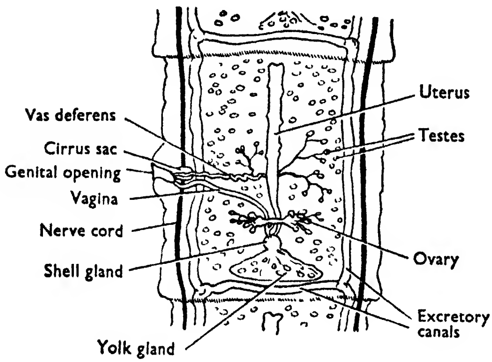


FIG 10.10.—A proglottis of *Tænia solium* with the reproductive organs fully developed, × 3.

Very little is known of the life of tapeworms. The body is highly contractile and varies tremendously in length. The food is unknown, but is presumably absorbed over the surface. They can live in very low concentrations of oxygen and produce fatty acids as well as carbon dioxide, but use oxygen when it is available.

REPRODUCTION

The reproductive organs have the same general structure as in the liver fluke : they are shown in Figs. 10.10 and 10.11. Each proglottis contains a complete set of them. Since no other worm is usually present, it must be fertilised either by another proglottis or by itself. From time to time the last proglottis breaks off, singly or with others, and passes out of the anus of the host. It is not able to crawl about, although that of the related beef tapeworm, *Tæniarhynchus saginatus* (=*Tænia saginata*) can do so, discharging

eggs as it goes. The eggs, to the number of 850,000 or more, are set free by the rupture of the proglottis wall. If, as may happen in various circumstances, they are now swallowed by a pig, or, as occasionally, by man, their shells are dissolved in the alimentary canal and a little spherical six-hooked embryo or oncosphere is set free from each. This bores its way from the intestine of the host into his blood vessels and is carried to the muscles and other organs, where it loses its hooks, increases in size, and becomes a bladder-worm or cysticercus. The wall of this becomes tucked in at one spot, forming a pouch, on the inner wall of which the suckers and hooks of the future head appear. This happens ten weeks after the egg has been eaten by the pig. No further change

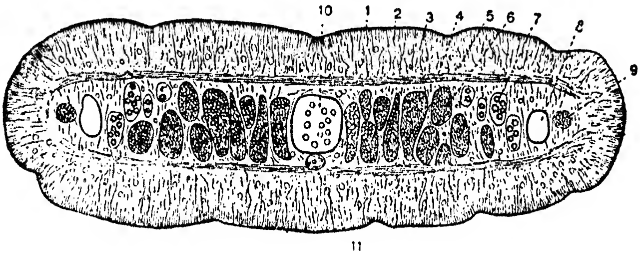


FIG. 10.11.—A transverse section through a proglottis of *Tænia* in which the reproductive organs are well developed.—From Shipley and MacBride.

1, Cuticle; 2, long-necked cells of ectoderm; 3, longitudinal muscle fibres cut across; 4, layer of circular muscles; 5, split in the parenchyma which lodges a calcareous corpuscle; 6, ovary; 7, testis with masses of male germ-mother-cells forming spermatozoa; 8, longitudinal excretory canal; 9, longitudinal nerve cord; 10, uterus; 11, oviduct.

takes place unless the flesh of a pig infested with such bladder-worms (known as 'measly' pork) be eaten raw or under-done by man. When this happens, the stimulus of the new surroundings causes the pouch to be turned inside out, the effective agent being the bile salts (p. 442) acting in a neutral or alkaline medium. This evagination cannot therefore occur until the intestine is reached. The bladder is digested, but the head fixes itself and begins to bud off proglottides. The life-history of *Tænia solium* may be summed up as follows :—

Egg→Oncosphere→Cysticercus→Scolex→Adult.

It will be seen that only one generation is involved, unless each proglottis be regarded as a complete individual, and not merely as a part of the parent body broken off to carry the eggs. Although the pig is the normal intermediate host, the eggs will develop in man, and heavy human infestations with bladder-worms are

known. The adult worm may live in man for more than twenty-five years.

PLATYHELMINTHES

The members of the phylum Platyhelminthes are adequately diagnosed as being triploblastic acœlomate Metozoa with no anus. In addition they are bilaterally symmetrical and dorso-ventrally flattened ; they have a flame cell or protonephridial system (a feature which they share with several other groups) ; and have characteristic complicated reproductive organs. There are no blood vessels.

CLASS I—TURBELLARIA

These are almost all free-living, and retain the gut, though this may be reduced and solid. The outer layer of the body consists of cells covered with cilia, by which the animals move on surfaces, although many of them also use muscles for this purpose and for swimming. In or just below the ectoderm are usually scattered cells containing peculiar rod-shaped bodies or rhabdites, of unknown function. There are sense cells of various sorts, mostly in the anterior part of the body, and usually eyes, which have the retina well-marked, but no lens. The nervous system (Fig. 10.12) is interesting and shows the beginning of a brain. There is a pair of ganglia in the head, united by a commissure and giving off longitudinal nerves to the body. These supply a nerve net under the epidermis and another deeper in the body. The function of this brain is merely to relay and distribute the impulses from the important sense organs on the head. Unlike *Hydra*, where no part of the body *permanently* dominates the rest, these creatures, moving as they do always with the same end forwards, have that end organised for perception and the constant stimulation of the rest of the body. This permanent organisation of a dominant region of the body unifies the reaction of the body as a whole to changes in its surroundings. But in the Turbellaria the brain does not co-ordinate the activities of different regions of the body. It sets them in action : that each plays its proper part is due to local organisation.

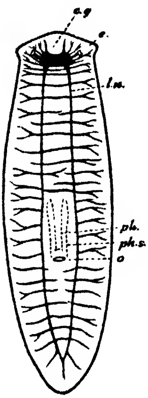


FIG. 10.12.—A diagram of the nervous system of a turbellarian.

c.g., brain ; *e.*, eye ; *l.n.*, longitudinal nerve cord ; *o.*, opening through which the pharynx is protruded : *ph.*, paarynx ; *ph.s.*, pharynx-sheath.

The Turbellaria are mostly carrion feeders, and protrude a long muscular pharynx, into which the food is sucked (Fig. 10.13). Two interesting features of them are their ability to regenerate when cut into pieces, and the fact that when starved they degrow. Not only do they decrease in size, but the internal organs are reduced and disappear in order, first the eggs and reproductive organs, and then the gut and muscles, the nervous system alone

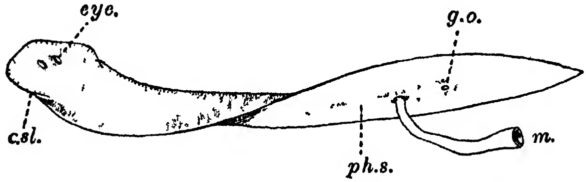


FIG 10 13 —A turbellarian (*Planaria polychroa*).—From Shipley and MacBride
c sl, Ciliated sensory slit at side of head, *eye*, *g o* genital opening *m* mouth, at end of outstretched pharynx, *ph s*, sheath into which pharynx can be withdrawn

being unreduced. When given food these starved animals regenerate their organs and return to their normal size.

The commonest British species of Turbellaria all belong to the Order Tricladida, in which the gut has three main branches. *Dendrocœlum lacteum*, *Planaria lugubris* and *Polycelis nigra* are all found in ponds and slow streams ; the first is white, and the other two black, but *Polycelis* has an anterior ring of eyes by which it may be recognised. *Planaria alpina*, also black, is found in mountain streams. *Procerodes litoralis* (=*Gunda ulvæ*) is marine and is found in rock pools. Some species are terrestrial.

CLASS II—TREMATODA

These are parasitic, or rarely epizoic. They have a thick cuticle, and suckers, and the adult has no external cilia. *Fasciola* is characteristic of the class, though its genital organs are more complicated than those of most species.

CLASS III—CESTODA

The tapeworms are entirely endoparasitic. There is no gut, and the ectoderm cells have sunk into the parenchyma, leaving a thick cuticle at the surface. Cilia are absent except for the flame cells. The characteristic form of the body of the adult is that with scolex and proglottides as shown by *Tænia solium*.

Other common tapeworms are : *Tænia saginata*, without hooks, found in man, with the bladder-worm stage in the ox ; it may be up to forty feet, or occasionally eighty feet long, and may have 2,000 proglottides ; *T. serrata* in the dog, with a bladder-worm in rabbits, hares, and mice ; *T. cœnurus* in the dog, with the bladder-worm known as *Cœnurus cerebralis* in the brain of sheep and

1.

2.

3.

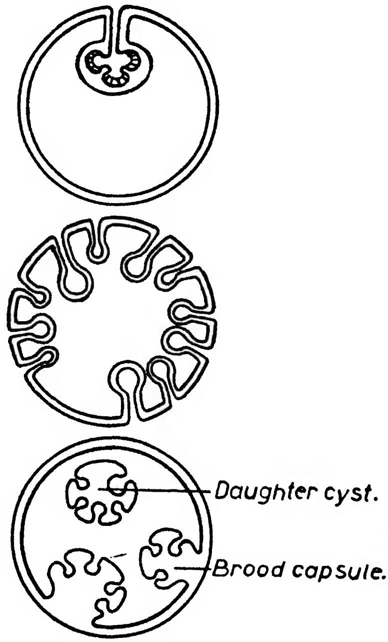


FIG. 10.14.—Diagrams of bladder-worms.

1. The ordinary Cysticercus type, with one head; 2. The Cœnurus type, with many heads; 3. The Echinococcus type, with secondary cysts or brood capsules producing many heads. Hooks and suckers are not shown in 2 and 3.

other hoofed animals, where it causes 'staggers'; and *T. echinococcus*, which has only three proglottides, in the dog, with the bladder-worm *Echinococcus* in sheep, oxen, pigs, and sometimes in man. The latter two species produce numerous heads in the bladder-worm stage. Since only one of these can be regarded as continuing the individuality of the bladder-worm, the others must be looked upon as buds from it, so that there is here a metagenesis. The bladder produced by *T. echinococcus* is known as a 'hydatid cyst'; it is very large, containing sometimes as much as a gallon of fluid, and its wall buds off secondary cysts into the cavity (Fig. 10.14).

11

ROUNDWORMS

BESIDES the flukes and tapeworms there is another group of parasitic worms, even more important medically and economically, and of at least equal biological interest. This is the group Nematoda, or roundworms, so called because in contrast to the flatworms their body is circular in cross-section, and so resembles a thread.

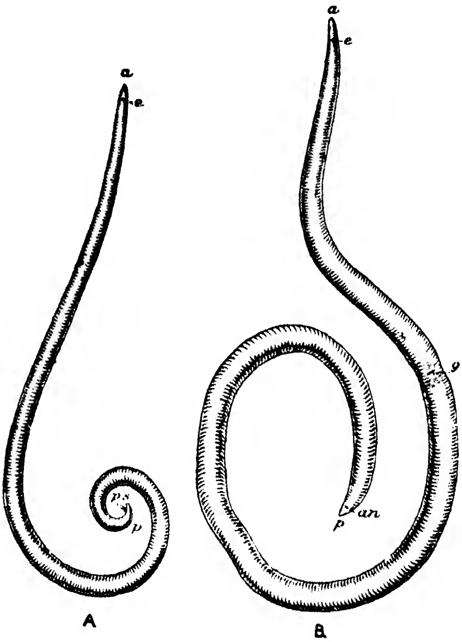


FIG. 11.1.—*Ascaris lumbricoides.*
A, Male; *B*, Female.
a., Anterior end; *an.*, anus; *e.*, 'excretory' pore; *g.o.*, genital opening; *p.*, posterior end; *p.s.*, penial setæ.

ASCARIS

Some of the largest roundworms are those belonging to the genus *Ascaris*. The species *suillæ* is frequently present in the small intestine of pigs, and *lumbricoides* (Fig. 11.1) is not uncommon in man, especially in children; the male may be as large as 17 centimetres long and 0·2 centimetres in diameter, while the female may be 25 centimetres by 0·5. *A. megalocephala*, which lives in the horse, is even larger. The following description is intended primarily for the human form, but will apply almost equally well to the others, which are indeed, according to some workers, merely physiological races of the human species.

The general shape is that of a cylinder with pointed ends, and the surface is smooth and yellowish-white in colour. Along the middle of the back and of the ventral side run white lines, and there is a brownish line along the middle of each flank. At

the front end is the mouth, guarded by three lips, one above and one at each side below. The dorsal lip bears at its base two papillæ and the ventro-lateral lips one each. The edges of the lips bear many small teeth, those of *suillæ* being smaller than those of *lumbricoides*. Median on the under side, about two millimetres from the mouth, is a so-called 'excretory' pore. The female bears a median genital pore at about one-third of the length of the body from the front end, on the ventral side of a region which is slightly narrowed. The tail is curved downwards, slightly in the female and strongly in the male. The anus lies below, about a couple of millimetres from the hind end. In the

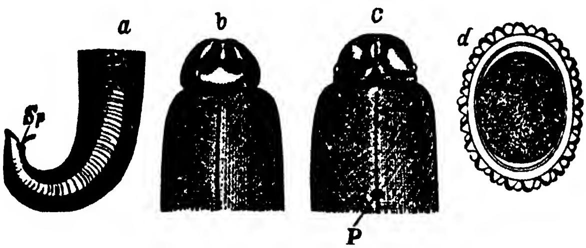


FIG. 11.2.—*Ascaris lumbricoides*.—From Sedgwick, after Leuckart.
a, Hind end of male; *b*, head, from above; *c*, head, from below; *d*, egg, in shell; *p*, 'excretory' pore; *Sp*, penial setæ.

male this opening serves also as a genital pore, and there project from it a pair of penial setæ.

Internally, a spacious perivisceral cavity separates a straight, simple gut from a simple body-wall. The cavity is traversed by numerous delicate strands of a remarkable connective tissue, which is composed of processes of a few cells, notably of one very large cell placed on the dorsal side just behind the nerve ring. Over the gut and the muscle fibres of the body-wall the strands join a thin covering layer which lines the cavity. Thus the body cavity may be regarded as intracellular, and is thus unlike that of other animals, which is either cœlomic or hæmocœlic (p. 187).

The body-wall is made up of three layers (Fig. 11.3): a stout, smooth cuticle, made of proteins, including collagen and some keratin, which consists of several layers and is shed four times, an ectoderm ('hypodermis') rich in glycogen, which is without cell-limits and must therefore be classed as a syncytium (p. 33), and a single layer of peculiar muscle fibres. The body-wall

contains a peculiar form of the red pigment hæmoglobin (p. 189), with a high affinity for oxygen, which is presumably used in respiration. Hæmoglobins are also present in other parts of the worm. The nuclei of the ectoderm, except at the hinder end, are

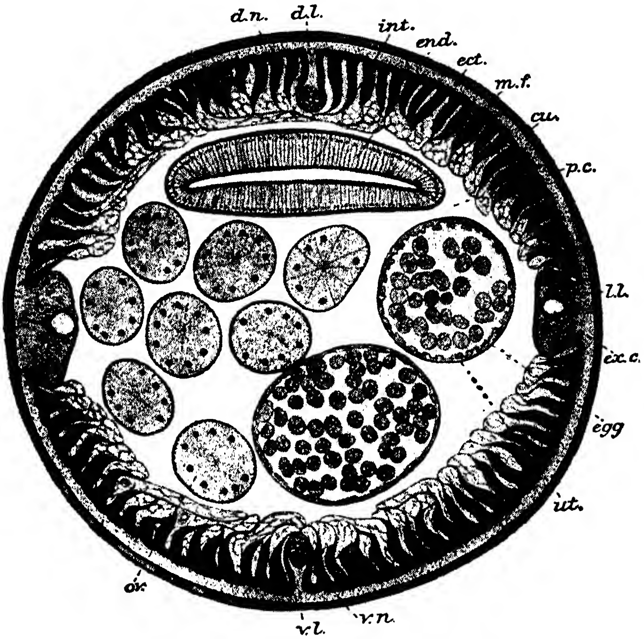


FIG. 11.3.—A transverse section through the middle of the body of a female *Ascaris lumbricoides*.

cu., Cuticle; *d.l.*, dorsal line; *d.n.*, dorsal nerve; *ect.*, ectoderm; *egg*; *end.*, endoderm; *ex.c.*, excretory canal; *int.*, intestine; *l.l.*, lateral line; *m.f.*, muscle fibre; *ov.*, ovary; *p.c.*, perivisceral cavity; *ut.*, uterus; *v.l.*, ventral line; *v.n.*, ventral nerve.

collected along the mid-dorsal, mid-ventral, and lateral lines. Along these lines the protoplasm bulges towards the body cavity. A nerve cord is embedded in the dorsal and ventral lines, and a canal in each lateral line. The canals have no internal openings; they unite in front to open by the execretory pore; in the free-living *Rhabditis* they have been shown to expel a fluid to the exterior. The two have but one nucleus, which is very large, and lies in the wall of the left-hand canal, near its front end. Thus they may be said to be hollowed in the body of one immense cell. Two more nuclei lie in the wall of the median duct to the exterior. Four very large, branched cells lie upon the lateral lines near the anterior end

of the body and have the power of taking up particles from the body cavity. They are known from this function as the phagocytic cells. The nerve cords (Fig. 11.4) are connected by transverse commissures in the ectoderm, and in front join a ring a little way behind the mouth. From this ring four other cords run back at the sides, and six forward. The nerve ring is slightly thickened above and rather more below, and contains some nerve cells. The only other ganglia are placed at the sides of the nerve ring and at the hinder end of the ventral cord. A few cells are scattered among the fibrils of which the cords are composed, but there is no sign of segmental arrangement in these or any other organ of the body. The number of cells which compose the nervous system is small and remarkably constant, each cell being recognisable in the same position in every individual. Each muscle fibre (Fig. 11.5) consists of an outer part which has fibrils running longitudinally and an inner part of undifferentiated cytoplasm containing a nucleus. Strands of protoplasm stretch from the inner parts of the muscle fibres to the dorsal and ventral nerves. The alimentary canal consists of three parts: a short stomodæum, or fore-gut, known as the pharynx, a long mid-gut, and a short proctodæum, or hind-gut,

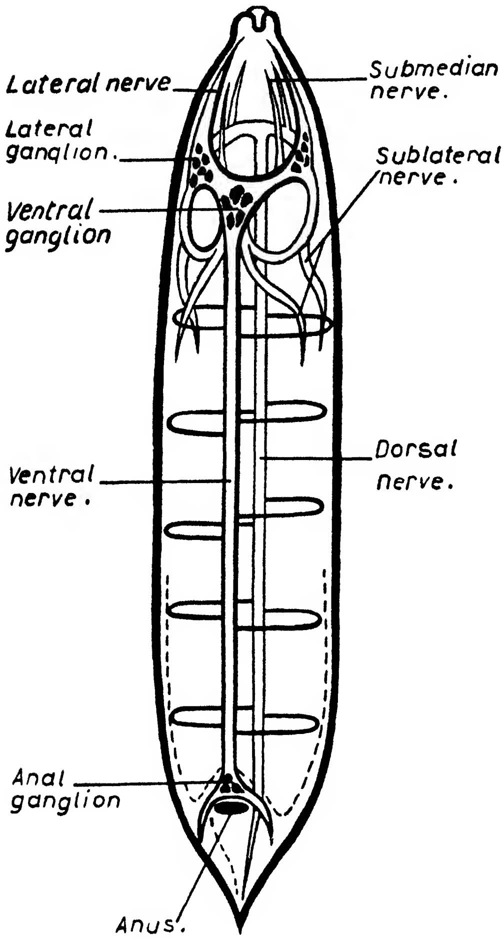


FIG. 11.4—A simplified diagram of the nervous system of a nematode.

known as the rectum. The fore- and hind-guts are lined by inturned ectoderm, with a prolongation of the outer cuticle, which is shed with the latter. They have in their walls muscular fibres. The mid-gut is composed solely of a layer of columnar epithelium, with a basement membrane outside it. The food consists of solids and liquids taken up from the contents of the intestine of the host.

There is neither vascular nor respiratory system.

REPRODUCTION

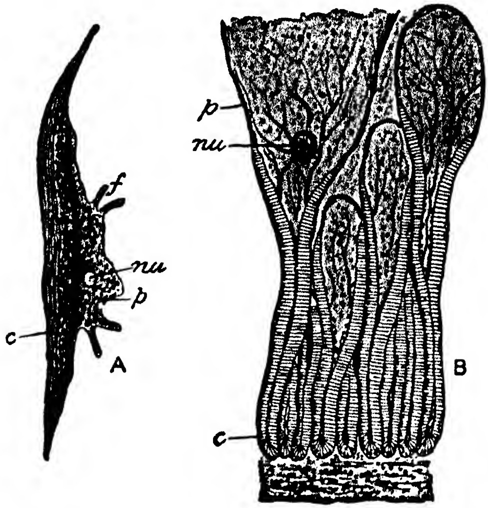


FIG. 11.5.—Muscle fibres of *Ascaris*.—From Parker and Haswell, after Leuckart. *A*, A single fibre; *B*, several fibres in transverse section, with a portion of the ectoderm (below); *c*, Contractile part of the fibre; *f*, processes; *nu*, nucleus; *p*, undifferentiated protoplasmic part of the fibre.

The genital organs (Figs. 11.6 and 11.7) are of a type peculiar to the Nematoda. They are paired in the female and unpaired in the male, and lie free in the body cavity. The male apparatus is composed of (*a*) the testis, a long, coiled thread consisting in its anterior part of a solid mass of immature sex-cells, and in its hinder part containing a cord or 'rachis' in the middle with riper sex-cells attached to it, (*b*) the vas deferens of much the same width as the testis, (*c*) the vesicula seminalis, a wider tube, (*d*) a short, narrow, muscular ejaculatory duct. The spermatozoa are simple rounded cells, which become amœboid when they have been transferred to the female. The female organs correspond with those of the male. Each ovary

has the same general structure as the testis, a hollow region which may be called the oviduct connects it with the wide uterus, and the two uteri unite in a short, muscular vagina. The eggs are produced in immense numbers—up to 200,000 a day—fertilised in the upper part of the uterus, enclosed in shell with an inner fatty layer and outer layers containing chitin and a protein, passed into the gut of the host, and by it voided with the fæces. Before they can bring about a new infection, they must pass through a period of ripening, which normally lasts thirty to forty days, and needs moisture, a temperature above 60° F., abundant oxygen, and the absence of putrefaction, and therefore cannot take place except in the outer world. The eggs survive poorly in heat or on drying, and in sandy soils they are washed to the surface and damaged. The most favourable situation for development is therefore a clay soil, in which they are protected, and, by being swallowed with food or water, may reach a new host. Usually they hatch in his intestine, but in warm, damp places may do so in soil. In the egg occurs the first of the four moults which *Ascaris*, like other nematodes, undergoes in the course of its life. The worms hatch as infective larvæ which in the new host do not at once become intestinal parasites but undertake first a remarkable journey.[1] Freeing themselves from the remains of the second cuticle and piercing the wall of the intestine, they enter venules and lymphatics (p. 452) and are carried through the liver and heart to the lungs, where they cause congestion and hæmorrhage and are thus discharged into the alveoli (p. 537). Thence they travel along the bronchi and trachea into the gullet and descend the alimentary canal to reach the intestine once more. In the lungs they undergo two more moults, and acquire as swimming-organs lateral membranes, which they afterwards lose, and grow from 0.28 mm. to 2 mm. in length. The final moult occurs in the duodenum, and a mature adult is formed four to five weeks after infection. The adult may live for a year.

Ascaris lumbricoides is found throughout the world, and can only be avoided by care taken in regard to the cleanness of raw foods and drinking water. It may cause little trouble to the host, or be the source of diarrhœa, anæmia and other complaints, the latter apparently through an enzyme formed by it which interferes with digestion. In severe infections with the eggs,

[1] Since they differ from the adults in nothing except size and the condition of the reproductive organs they are strictly not larvæ but nymphs (p. 244).

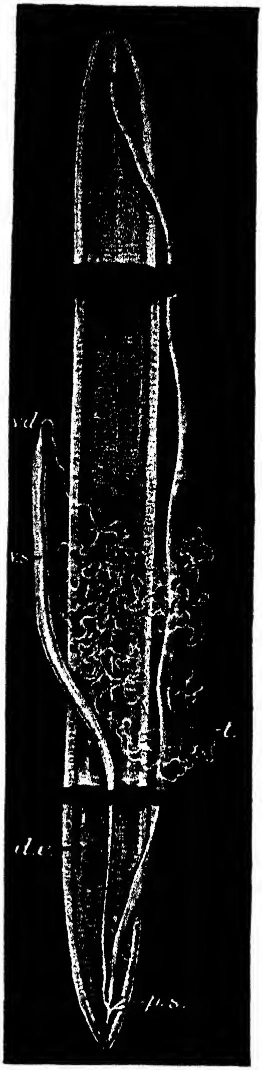


FIG. 11.6.—A male *Ascaris lumbricoides* dissected from above.

d.e., Ductus ejaculatorius; ***p.s.***, sacs of the penial setæ; ***t.***, testis; ***v.d.***, vas deferens; ***v.s.***, vesicula seminalis.

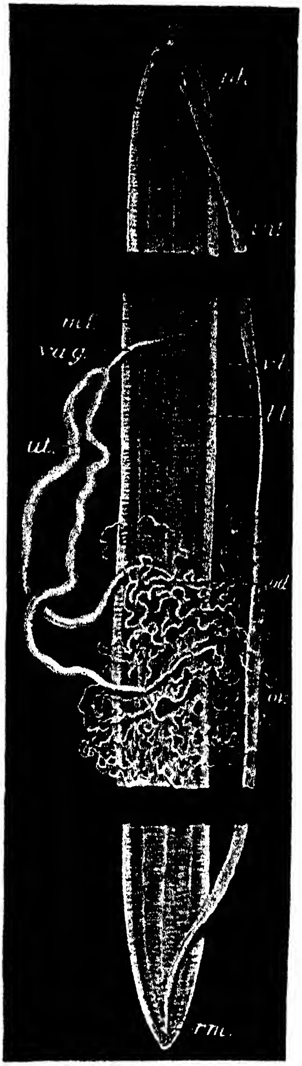


FIG. 11.7.—A female *Ascaris lumbricoides* dissected from above.

int., Intestine; ***l.l.***, lateral lines; ***m.f.***, muscle fibres; ***od.***, oviduct: ***o v.***, ovary; ***ph.***, pharynx; ***rm.***, rectum; ***ut.***, uterus; ***vag.***, vagina; ***v.l.***, ventral line.

temporary bronchitis may occur during the passage of the larvæ through the lungs. Santonin, thymol, and other vermifuges are used against the worm.

OTHER ROUND WORMS

Though many nematode worms are known, none of them has been found to differ anatomically from *Ascaris* in any important respect : this is remarkable, because while some are parasitic in vertebrates, others live in invertebrates, some parasitise plants and yet others are free-living, so that one type of structure serves for a wide variety of habitats. Their life-histories, however, although nearly always including four larval moults, are as diverse as they are remarkable. The following are examples :—

1. *Free-living throughout life.*—One of the best-known examples is *Rhabditis aberrans* (Fig. 11.8), which is about one mm. long and is common in soil. It is saprozoic, feeding on decaying organic matter, although some species may invade the roots of plants. The adult is easily observed as a transparent object under the microscope, when it can be seen that the œsophagus shows active muscular pumping movements while the contents of the mid-gut are moved only by the general contractions and bendings of the body in locomotion. The genital organs are simpler than those of *Ascaris*. Copulation takes place, and the eggs are laid. After the second moult the larva may remain within the shed skin, in an apparently encysted condition. It retains the power of movement, but can resist desiccation and so serves as a distributive and dormant stage. Larvæ of some species in this state may attach themselves to dung beetles and other insects and so be distributed. In some species of *Rhabditis* the males are few and sexually degenerate, while the females have developed into protandrous hermaphrodites.

Other genera in the soil, such as *Mononchus*, are predators, feeding on small worms and other nematodes. Another free-living species is *Anguillula aceti*, found in vinegar.

2. *Free as larvæ, parasitic on plants as adults.*—The Cockle Worm, *Anguina* (=*Anguillulina*=*Tylenchus*) *tritici* (Fig. 11.9) causes ear-cockles in wheat. A pair, living in a single flower of the plant, become mature in late summer, and produce hundreds of larvæ. The plant tissues react by forming a gall (the cockle) instead of a proper fruit, and in this the larvæ may survive for

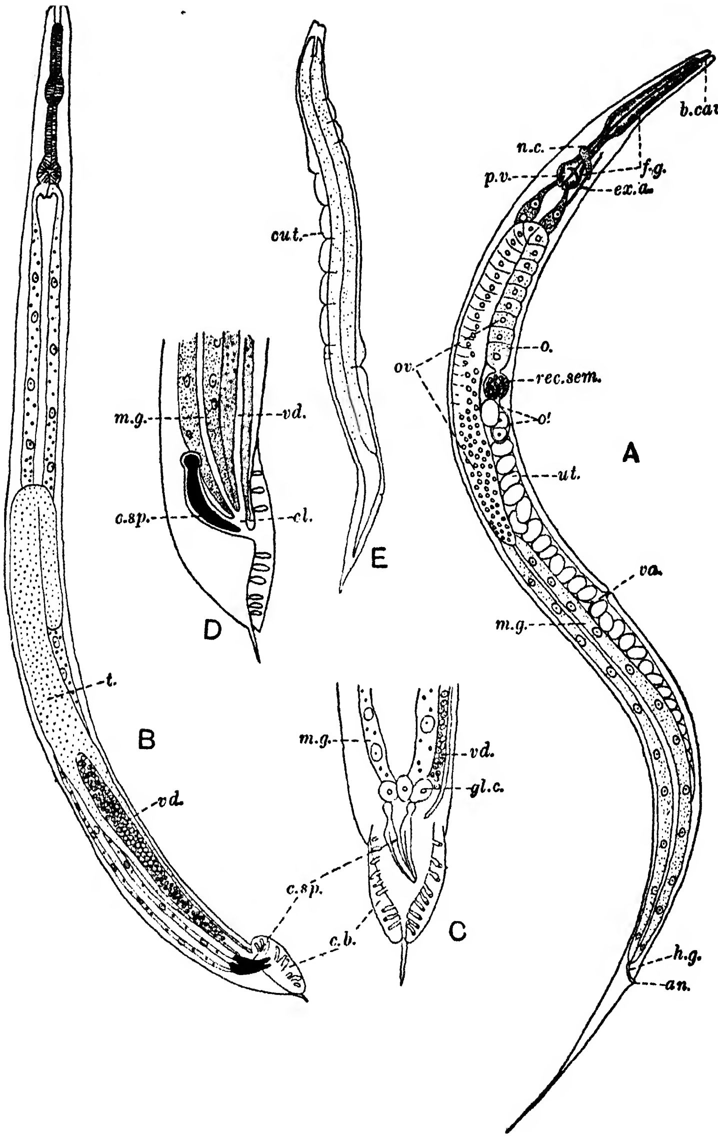


FIG. 11.8.—*Rhabditis*.—From Borradaile and Potts, *The Invertebrata*, 2nd edition, 1935. Cambridge University Press.

A, Mature female; *B*, mature male; *C*, ventral view of hind end of male, slightly turned to one side; *D*, side view of hind end of male; *E*, encysted larva; *an.*, anus; *b.cav.*, buccal cavity; *c.b.*, copulatory bursa; *c.sp.*, copulatory spicule; *cl.*, cloaca; *cut.*, stretched skin of the last larval moult; *ex.a.*, excretory aperture; *f.g.*, fore-gut; *gl.c.*, gland cells; *h.g.*, hind-gut; *m.g.*, mid-gut; *n.c.*, nerve collar; *o.*, egg ready to be fertilised; *o'.*, eggs fertilised and in 2-cell stage; *ov.*, ovary; *p.v.*, pharynx; *rec. sem.*, receptaculum seminis; *t.*, testis; *ut.*, uterus; *va.*, vagina; *vd.*, vas deferens.

ten years. In damp earth, however, they become active and escape. In the spring the larvæ crawl up a young wheat plant, and live among the leaves surrounding the growing point; they finally enter the flowers, where the life-cycle begins again.

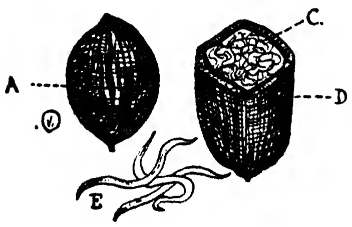


FIG. 11.9.—The corn-cockle worm From Theobald.

A, Cockle gall; *C*, larvæ; *D*, gall cut open *E*, larvæ magnified.

The second-stage larvæ of *Heterodera* are at first free, and then infect the cortex of the roots of tomato, cucumber or other plants. The females grow into lemon-shaped adults that live ectoparasitically on the roots, while the male adults are normal in shape and free-living so that they can wander and fertilise the females.

3. *Free as larvæ, parasitic in animals as adults.*—*Ascaris* is one example of this type; another is *Ancylostoma duodenale*, the hookworm (Fig. 11.10), which is pink, and lives in the small intestine of man. The male is 8–11 mm. long, the female 10–18 mm. It browses on the tissues, and so causes a considerable anæmia. Copulation

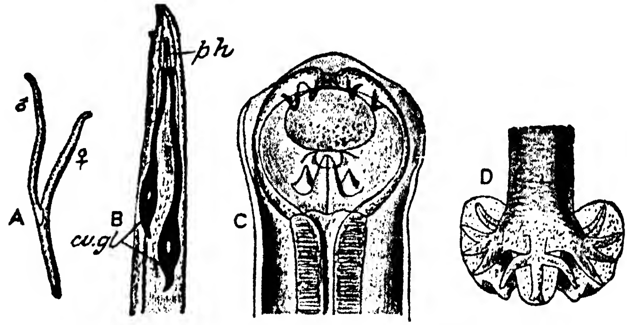


FIG. 11.10.—The hookworm (*Ancylostoma duodenale*).—From Parker and Haswell, after Leuckart.

A, Male and female *in coitu*; *B*, anterior end; *C*, mouth. with spines; *D*, hinder end of male, with expansion known as *bursa*; *cv.gl.*, cervical glands; *ph.*, pharynx.

occurs, and the eggs are laid and are passed to the exterior having divided to the four- or eight-cell stage. Further development requires air, moisture, a moderately high temperature, and preferably darkness. In temperate climates they can therefore only grow in such places as mines and tunnels, which has led to the animal being known in this country as the miners' worm, and the disease which it causes as miners' anæmia. In

all tropical and sub-tropical countries, however, the worm is widespread, as the larvæ can develop in the open. The third-stage larva, which as is usual in nematodes is the infective or wandering stage, is reached in about a fortnight. It remains within the second larval skin, and can penetrate through the skin of any part of the body of man. The foot is a common site in countries where shoes are not worn, and larvæ on salads or in drinking water may enter through the membrane of the mouth. Having pierced the skin, the larva enters a venule or a lymphatic, and goes by the veins to the right side of the heart and to the lung. It is too large to enter the capillaries, and so pierces the lung walls and passes into a bronchiole, whence it crawls up the trachea and is swallowed. It acquires a temporary capsule in the stomach, and after two more moults is adult. The hooks by which it attaches itself to the intestinal wall are acquired at the third moult. The period from infection to the appearance of eggs in the fæces is about eight weeks.

4. *Larvæ parasitic, adults free.*—This is a reversal of the common state of affairs. *Mermis nigrescens*, the female of which may be 20 cm. long and the male a quarter of that, also illustrates the Nematoda parasitic solely in invertebrates, although there are others in which the life-cycle is more normal. The adults live in soil and also climb the stems of plants to a height of two feet or more, especially after June showers, so giving rise to the English name of 'rain worm'. The eggs are laid on the plants and are eaten by phytophagous insects such as earwigs and grasshoppers. The larvæ penetrate the body cavity and finally emerge, usually killing their host, and return to the soil. In other species the larvæ penetrate the insect from outside.

5. *Larvæ and adults parasitic in different animals, with a free stage.*—An example is the Guinea Worm, *Dracunculus medinensis*, the female of which may be three or four feet long. The posterior part of the gut is lost and there is no anus, and almost the whole body is occupied by an expanded uterus containing larvæ. These escape, either through a female genital opening or vulva just behind the mouth, or through the mouth itself, while the host is immersed in water. The larvæ must penetrate a crustacean of the genus *Cyclops* (p. 234), and here they develop for three to five weeks, with two moults. If a man drinks water containing infected *Cyclops* the larvæ are released, and bore their way to the sub-cutaneous tissue. As the worm grows it goes towards the

extremities, especially the ankle, and here the head comes near the surface and is exposed in a small ulcer. It is the contact of cold water with this which stimulates the liberation of the eggs. The male is shorter than the female and has rarely been seen. The worm infects man in many tropical countries.

6. *Larvæ and adults parasitic in different animals, with no free stage.*—The best-known of these is *Wuchereria* (*Filaria*) *bancrofti*, the cause of elephantiasis, which is found in all tropical countries and as far north as southern Spain. The females are about four inches long, the males half this size, and both live in the lymphatics of man. The female is ' ovoviviparous ', that is, the egg-case contains a completely formed larva. This is set free and goes to the blood, where it lives for some time and is known as a *Microfilaria*. The larvæ congregate in the peripheral blood vessels at night, retreating to the capillaries of the lungs and to neighbouring vessels during the day. In due course the host is bitten by a gnat, and some of the microfilariæ are sucked up. They develop for about a fortnight, and may then be passed to a new host when the gnat next bites. They are carried by several species and genera of gnats, including the common *Culex pipiens*. Other species of *Filaria* have somewhat similar life-histories, with different invertebrate vectors ; *F.* (=*Loa*) *loa* is carried by the tabanid fly *Chrysops*, and *F. perstans* by a leech.

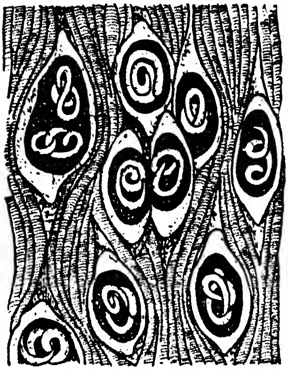


FIG. 11.11.—*Trichinella spiralis*, young encysted in muscle of host. — From Thomson, after Leuckart.

7. *Adult and larvæ parasitic, without free stage, in the same or a closely related species of host.*—*Trichinella spiralis* lives as an adult in the small intestine of man, rat, and pig, and some other mammals, and experimentally even salamanders may be infected. The males are a millimetre long, the females three or four millimetres. The male dies soon after copulation, but the female bores into the lymphatics and produces many larvæ, which are carried in the general circulation to the muscles and there encyst (Fig. 11.11). A new host is infected if it eats meat containing the cyst. The commonest natural cycles are rat/rat, rat/pig, and pig/rat, but man may be infected if he eats raw pork (as in German

sausages) or even that which is underdone. The worms in the intestine cause general intestinal symptoms resembling those of typhoid, and the encysted larvæ produce general weakness and often death.

8. *Parasitic in vertebrates, no larval stage.—Trichocephalus* (=*Trichuris*) and *Enterobius* (=*Oxyuris*) (Fig. 11.12) are medically unimportant inhabitants of the human gut, the former about an inch long, the latter half an inch in the female and an eighth in the male. Eggs pass out with the host's fæces, and may be swallowed with raw vegetables. Those of *Enterobius* are ripe as soon as they reach the exterior, so that reinfection by scratching often takes place.

9. *A free bisexual generation alternates with a parasitic hermaphrodite.*—The hermaphrodite stage of *Rhabdias bufonis* (=*Rhabdonema nigrovenosum*) lives in the lungs of the frog. It is protandrous. Embryos escape by the glottis and cloaca, and become sexual adults. The young produced by these wander, and may be swallowed by another frog.

The nematodes are an isolated and uniform group. They show certain superficial resemblances to arthropods (ecdysis, absence of cilia, absence of cœlom, unflagellated sperms), but these are not enough to justify the suggestion that the parasitic forms are degenerate arthropods and the free-living species descended from the parasites. There are many important differences, and it seems best to regard the nematodes as fairly primitive forms which never possessed a cœlom. Their success at their own level is obvious.

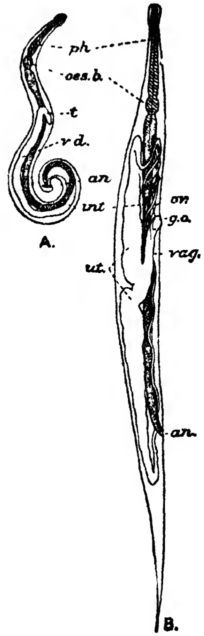


FIG. 11.12 —*Oxyuris*, somewhat diagrammatic, to show arrangement of organs.

A, Male; *B*, Female.

an, Anus, *g.o.*, genital opening; *int.*, intestine; *oes.b.*, bulb of œsophagus; *ov.*, ovary; *ph*, pharynx; *t.*, testis; *ut.*, uterus; *v.d.* vas deferens, *vag*, vagina.

12
PARASITISM

PARASITISM is a very strange mode of life, and as the nematodes include some of the most successful, as well as most important, parasites in the animal kingdom, it is convenient to discuss here some of the generalisations that can be made on the subject.

A parasite is generally formally defined as an organism which lives in or on the body of another to the detriment of the latter, but any such definition brings one into trouble at once. It is best to make definitions, if such must be made, of the relationships rather than of the relatives. It is clear as soon as one studies the animal kingdom that most species of animal stand in some sort of special relation to one or more other species, and what we are trying to do is to set limits and give names to these relations. (A similar argument can be applied to plants but it is not relevant here.)

The simplest relationship is that where one animal merely uses another as a base on which to stand, as barnacles often grow on the shells of limpets, and the ciliate *Kerona* runs about on *Hydra*. So far as is known neither has any effect on the other. The nomenclature of this sort of relationship is imperfect, but on the analogy of epiphytism it might be called epizoonism, and the animal which is supported an epizoon. A stage beyond this is commensalism, where two animals live in close physical proximity so as to be mutually helpful; since the partnership is equal, each member may be called a commensal. The small hermit crab *Eupagurus prideauxi* often carries on its mollusc shell an anemone, *Adamsia palliata*, which finally dissolves the shell and takes its place, so saving the crab from having to move house; it also protects the crab by its nematocysts. In return it acquires the advantages of locomotion and receives as food scraps which fall from the mouth of the crab. The syrphid flies which scavenge in the nests of bees, and the aphides tended by ants, are other examples.

A partnership for mutual benefit where the advantages and association are intimately physiological is called symbiosis, and the partners are symbionts. It is often probable that the benefits are rather one-sided. Though the relation between *Chlorohydra viridissima* or the corals and their green Algæ is generally called symbiosis, the advantage that the cœlenterates derive from the plants is unknown. They seem not to use the carbohydrate

produced by photosynthesis, and indeed starved corals expel their guests. The plant cells presumably acquire carbon dioxide and perhaps other end-products from the animals, and it may be an advantage for these to be quickly removed. A clearer example of symbiosis is given by the flagellates which live in the gut of termites, and so enable those insects to live on wood. For their part, the termites do a preliminary breaking down and softening of the food.

Where one partner gets all the benefit, and the other almost inevitably suffers some disadvantage, we have parasitism. It is generally recognised that the line between commensalism and symbiosis on the one hand, and parasitism on the other, is often blurred, but it is not so often realised that it is equally difficult to distinguish a parasite from a carnivore. Although we seldom put it into our definitions, the assumption that a parasite is smaller than its host is implicit in our thinking; we call a flea or a leech a parasite, a spider, which also feeds on the juice of prey which is at first living, a carnivore. Parasites do not in general kill their hosts, or at least not very quickly, but many do, and there is at least one carnivore which does not. Grebes on the Lake of Tiberias feed on the eyes of large fish, which they bite out of the head, while the fish, though blinded, go on living. The association of parasite with host is usually longer in time than that of carnivore with prey, but there is in fact a complete series from parasites which take only an occasional meal to those which cannot live away from the host (or hosts) at all. For the Insecta, for example, Keilin has drawn up the following list:

1. *Aedes*, a gnat which needs no blood but will take it if it gets the chance.

2. *Anopheles*, a gnat of which the female needs occasional blood meals before it lays eggs.

3. *Stegomyia*, a gnat which needs frequent blood meals.

4. *Cimex*, the bed bug, which feeds on nothing but blood, drops off the host after a meal, but remains near him.

5. *Pulex*, the flea, does not often leave the host, and dies if kept away for long.

6. *Pediculus*, the louse, remains on the surface but moves about.

7. *Phthirus*, the crab-louse, moves very little.

8. *Sarcopsylla*, a flea of which the female burrows into the skin and lives permanently in a tumour.

9. The larvæ of *Hypoderma*, the warble fly, and of some other Diptera, are completely internal. It is impossible to complete

the series within the Insecta, but we have already seen various degrees of independent life in the nematodes, and have met examples of this group and of Protozoa where there is no free-living stage in the life-history at all.

If we are to have a definition of a parasite which has any practical value, we must extend the usual one by several clauses. A parasite may be defined, with some approach to accuracy, as an animal which, for an appreciable time, lives in or on the body of another, considerably larger, animal, called the host, to the detriment of the latter, but without causing its death until reproduction of the parasite has occurred. This leaves the zoologist free to put his own meaning on 'appreciable time' and 'considerably larger'. Having digested this definition you may remember that ornithologists agree in calling the cuckoo a parasite, although it lives neither in nor on the body of the host, and so far from feeding on the host, is voluntarily fed by it.

Since parasites are generally small it is not surprising that few members of the phylum Chordata, all the members of which are relatively large, have adopted the habit. The teleost *Remora* attaches itself to larger fish for the sake of transport, and the hagfishes (p. 549) bore their way into the bodies of dead or dying fish, so that they are on the borderline between parasitism and carnivorous life. The only true vertebrate parasites seem to be the little fish known as fierasfers. The best known of them, *Carapus apus*, has a larva which enters the anus of a holothurian and feeds on its tissues. In this stage it is an obligate parasite and cannot find its way back into its host if it is removed. It metamorphoses, and the adult can, and does, leave and re-enter its host's gut, finding its way by a combination of visual, tactile and chemical stimuli. It feeds both inside and outside its host.

The rarity of parasitism in some phyla, such as the Cœlenterata, and its absence from others, such as the Porifera and the Echinodermata, remains unexplained.

Fortunately, although few biological terms can be rigidly defined, the general meaning is often clear. This is true of the term parasite, and it is the typical parasites that we must now consider. In the first place, it is convenient to divide them into ectoparasites which live on their hosts, and endoparasites which live in them, although, as we have seen, there are intermediate forms. The modifications in both form and physiology which are

necessary in parasites differ in these two groups, as do their effects on their hosts.

EFFECTS ON HOSTS

The effects of parasites on their hosts make up much of the subject-matter of pathology, and it is impossible in a textbook of zoology to go far in their study, but some generalisations are possible. It is often said that the successful parasite does not kill its host, and even that the really successful parasite does not even harm it, but there does not seem to be any justification for this view. Judged by their ubiquity, malarial parasites and *Trichinella* are highly successful, but they often cause death; the ichneumon flies which live in the caterpillars of Lepidoptera also appear to be highly successful, but they always completely consume their host. It is true that there must be a limit to the power of the parasites to kill, for if all hosts were killed there could be no parasites, but in fact the reproduction of the hosts seems to keep pace with the deaths, and a low density of population inevitably means a smaller chance of infection, which makes the host-parasite ratio to some extent self-regulating. It is this which may account for the violent fluctuations in numbers of many animals, especially rodents. The numbers of voles, for instance, increase steadily until a certain degree of overcrowding is reached, and then an epidemic caused by a parasite spreads rapidly and reduces the numbers.

Apart from death, the effects on the hosts vary with the parasite and the place where it lives. Ectoparasites seldom cause more than irritation, although secondary infection with another parasite, such as the *Plasmodium* carried by the gnat, may lead to serious results. Endoparasites which live in the gut (which, strictly, is outside the body) may do nothing more than deprive the host of some food; such is the case with a small number of *Ascaris* or tapeworms; larger numbers may take so much food that the host cannot supply enough, with general effects on health, and symptoms such as diarrhœa and vomiting are common. Hookworms may cause enough loss of blood to produce anæmia. Parasites living in the fluid tissues (the blood and lymph) may merely steal some food, as does *Filaria perstans*, which produces no known pathological effect; they may mechanically block the vessels, like *Filaria bancrofti*; or, like *Trypanosoma*, and *Plasmodium*, they may manufacture toxins which cause a

violent reaction in the host. Those which live in the solid tissues, such as the Guinea worm and *Trichinella*, always cause irritation, and may have more serious effects. A special case is made by those parasites which preferentially attack the gonads, causing parasitic castration. Examples are known in the Protozoa, trematodes and insects, but the most familiar is the cirripede crustacean *Sacculina*, parasitic on crabs, in which the castration is accompanied by changes in the secondary sexual characters. Parasites which attack the brain, such as *Trypanosoma* in its later stages, and the cysticercus of *Tænia cœnurus* in sheep, have profound behavioural effects. According to the situation and degree of toxicity of the parasite, various local reactions, from inflammation to tumours, may occur in the host's tissues.

IMMUNITY

A matter which is of great importance both to the parasite in its efforts to establish itself in a new host and to man in his efforts to combat disease, is the degree of immunity which the host shows to the parasite. The word 'immunity' is used in a wide sense to cover a number of different modes of reaction. At the one extreme, host restriction and other difficulties in infection may be determined simply by the fact that the ordinary conditions of the environment are not suitable for the development of the parasite. Very often the egg-shells or cyst-cases of intestinal parasites must be digested so that the embryo is liberated; we have seen that this is so in tapeworms, and it is true also of many Protozoa, such as the sporozoan genus *Eimeria*, various species of which are common parasites of domestic animals, with no very great degree of host restriction. The cysts of *Eimeria* from fish, however, when ingested by man, are unaffected by his digestive enzymes, and pass right through and remain alive in the fæces. Live proglottides of tapeworms cannot infect man, because the egg-shells need the successive action of acid and bicarbonate, and unless the proglottis is first killed, the eggs are not liberated, and so exposed to the digestive juices, until the intestine is reached and the acid of the stomach has been left behind.

At the other extreme, there may be an active warfare of the host against the invading parasite, and it is this that we most commonly think of as immunity. It takes two chief forms. In the first, which may be called the cellular mechanism, amœboid

cells of the host, called phagocytes, actively ingest and digest the parasites. Phagocytes are found chiefly in the blood (the polymorphonuclear leucocytes; see pp. 529–30) and in connective tissue (macrophages; see p. 518). In the second, the chemical or humoral mechanism, the presence of the parasite causes the production of substances which have a specific action on the things which bring them into being. This is a particular example of the general effect of the introduction of a foreign protein or carbohydrate of large molecule into the tissues. Such a substance, called an antigen, induces the formation of a specific antibody. This may act in any of three main ways; it may merely neutralise the objectionable effect of the antigen (the antitoxic effect), it may render the parasite more vulnerable to the attack of phagocytes (opsonification), or it may itself bring about the death and destruction of the invader (lysis). Antibodies acting in these ways are called antitoxins, opsonins, and lysins respectively.

There are also substances which act in the same way called natural antibodies, because they are naturally present, and they could obviously assist in host restriction (p. 153), but they are less interesting than those which only develop in the presence of the parasite and so confer an acquired immunity. It seems to be on the whole rare for a host to acquire complete resistance or immunity to an animal parasite, that is, to develop such a chemical reaction that it cannot subsequently be infected by the same species. Cattle may, however, acquire a resistance to *Trypanosoma brucei* and others, and man to *Plasmodium vivax*. Partial resistance to the cysticercus stage of tapeworms, is common, but resistance to the adults is probably never acquired. A peculiar form of resistance, called premunition, does, however, prevent a second infection in a man who harbours a single beef or pork tapeworm, and premunition also prevents subsequent infection with Protozoa in a number of animals and diseases, including malaria and trypanosomiasis, so long as any individuals derived from the first infection are present; these are themselves also kept in check. Many bacteria confer a much stronger immunity, so that all the original invaders are killed, and reinfection is impossible for long afterwards.

EFFECTS ON PARASITES

In attempting to determine the effects which parasitism has had on parasites one must compare them with what appear to

be their nearest free-living relatives. This is easy with insects like the warble-fly or the ichneumons, where parasitic larvæ grow into normal adults, or the crustacean *Sacculina*, where the parasitic adult is formed from a normal nauplius larva, but in the more typically parasitic groups it is more difficult. Neither the Sporozoa nor the Trematoda nor the Cestoda are at all closely related to other members of their phyla, and though there are free-living nematodes they seem to differ not at all from the parasites. The 'adaptations to parasitism' of elementary textbooks and examination papers are, in fact, mostly imaginary; there is no evidence that any parasite possesses any physiological mechanism or structural peculiarity that is not possessed or paralleled by free-living animals. What is true is that parasites show an unusual development of features which are known elsewhere. While the few parasitic members of the 'higher' groups, chiefly the Crustacea and Insecta, have lost almost all their characteristic features, many parasitic ciliates and flagellates show a structural complexity unapproached by the free-living forms.

Ectoparasites generally possess piercing and sucking mouthparts, for they typically feed on blood; the Mallophaga or bird lice are exceptional in feeding on feathers which they seize with biting mouthparts. Often ectoparasites also possess some means of attachment, such as the posterior sucker of leeches and the well-developed claws of lice. Gut-living endoparasites also often possess means of attachment, such as the hooks and suckers of tapeworms and the jaws and sucking mouth of the hookworm; most nematodes, however, have none. Many parasites possess at some stage of their life-history considerable powers of locomotion, as the frequent occurrence of the sentence 'bores its way into the tissues' in the accounts of life-histories shows. Once in place they may not move, but they have seldom lost any organs of locomotion other than those specially developed for the use of the larvæ. The flatworms show a progressive loss of cilia. The uniform environment in which many parasites live, at least as adults, presumably means that they receive few stimuli, and one might therefore expect there to be few sense organs. This is found to be true, but at the level of body-organisation of the three major parasitic groups there would be few sense organs anyway. The ability of the Guinea worm to get its head to the right place at the right time suggests a co-ordinated response of a high order.

Most parasites are well supplied with food, and often this is

of a simple form ; in the small intestine and in the blood stream there are hexoses and amino acids in place of the polysaccharides and proteins which are all that most free-living forms can get. Parasites in such situations therefore need few if any digestive enzymes, and can begin synthesis or oxidation straight away ; it is tempting to connect the absence of the gut from the cestodes with this, but it must be remembered that the free-living Platyhelminthes show a progressive degeneration of the gut, and that some of the turbellarians have it replaced by a solid mass of cells. It seems, therefore, that parasitism need not have caused the absence of the gut from the tapeworms, but that the parasitic mode of life allowed an innate tendency to go to an extreme. Most nematodes have a well-developed gut wherever they live. Parasites such as the hookworms, which eat the tissues, are in no different case from any animals to whom food comes easily. It is possibly the large food supply that has induced the large reproductive capacity of parasites, for it is a general observation that much food means many eggs. Pelagic fish, the queen honey bee, and the barndoor hen are non-parasitic examples. Parasites have as much need to excrete as have any other animals, for it cannot be expected that the amino acids of their food will exactly fit their own tissues. *Fasciola*, *Tænia*, and *Ascaris* have all been shown to produce much ammonia, which is the normal nitrogenous excretory product of aquatic species.

Contrary to common belief parasites do not generally live in an atmosphere devoid of free oxygen. It is obvious that those living in arterial blood have plenty, and even in venous blood and in the tissues there is no mean amount. The partial pressure of oxygen in vertebrate tissue ranges from 10 to 45 mm. of mercury (that of the atmosphere is about 150 mm.). As this is largely produced by the dissociation of oxyhæmoglobin, which acts as an oxygen store, it represents a quantity of oxygen far greater than would be available in the same volume of most natural waters. There is no reason to expect that parasites would respire in a different manner from other simple animals or the tissues of the host, and experiments have confirmed the similarity. Parasites use oxygen when they can get it, and most of them have plenty of opportunity of doing so ; when it is not available they respire anærobically, just as does vertebrate muscle, by a breakdown of carbohydrate, especially glycogen. Lactic acid is often produced, valeric (=valerianic) acid ($CH_3CH_2CH_2CH_2COOH$) is

even commoner, and *Trichinella* rather oddly produces carbon dioxide anærobically without any organic acids at all. This worm is also peculiar in that the adult has no glycogen. The difficulties of culturing most parasites outside their hosts are great, but it appears from a good many experiments that absence of oxygen lowers activity and reduces survival time. The lumen of the gut differs from all other parasitic habitats in sometimes having a very low oxygen concentration, though it is no lower than is often found in other natural habitats, such as the mud of ponds. It is here, if anywhere, that we should expect to find parasites that can live without oxygen and *Ascaris*, for example, seems to need and use only a small quantity; the Protozoa which live in the rectum of many vertebrates probably get very little oxygen, and probably come as near as any animals to being anærobic. There is, however, no reason to think that they are completely without oxygen, or that they cannot use what they do get; since so ærobic a tissue as mammalian skin epithelium can survive under strictly anærobic conditions for a week, there is no need to postulate any peculiar type of life for the parasites.

A feature of their life which parasites share with the inhabitants of small ponds is that their ecological niche is discontinuous and short-lived. Like pond animals therefore they need a distributive phase. We have seen many instances where this is an egg or an encysted larva, but most interesting are those where a second host acts as an intermediary. This may itself be an ectoparasite, like the gnat which carries *Plasmodium* or *Filaria bancrofti*, or it may be the food of a carnivorous host, like the *Trichinella*-infected rat eaten by a pig. In strict usage the host which harbours the sexual phase is called primary, the other secondary, but where there is no sexual phase, as in trypanosomes, or often for medical reasons, man is considered as the primary host. Parasites generally produce many eggs, which may, as has been said above, be merely the result of their good food supply. When the large numbers of parasitic nematodes, almost all of which are bisexual, are considered, it is very doubtful if hermaphroditism is any commoner amongst parasites than in the animal kingdom as a whole. It is obviously not necessary for success, and it is difficult to see how, without self-fertilisation, it could be of any advantage. Even hermaphrodite parasites such as the liver fluke and tapeworm have well-developed copulatory organs, suggesting that cross-fertilisation is either still practised or has only recently been given

up. It should be noticed that hermaphroditism is much commoner in free-living nematodes than in the parasitic species.

There remains to be considered the chemical relationship between parasites and their hosts. This has two aspects. In the first place gut parasites, and to a lesser extent those living elsewhere, are exposed to enzymes which might at first thought be expected to attack the parasites and dissolve their cells; this would seem to be especially likely with worms in the small intestine exposed to trypsin. It is clear that the worms survive, and it can be shown that neither trypsin nor pepsin has any effect on them so long as they are alive. The same is, however, true of living earthworms, arthropods, fish, and Protozoa, so that it seems that the living cell surface of all animals is not attacked by, and is impermeable to, proteolytic enzymes. Over and above this, however, some parasites produce anti-enzymes, which diffuse into the medium and neutralise the enzymes there present. The evidence for tapeworms is conflicting, but it seems certain that *Ascaris* produces, or causes the production of, a substance which combines with and neutralises trypsin (and pepsin). It is a polypeptide, and it so closely resembles an anti-enzyme extracted from beef pancreas that it has been suggested that it is not formed by the worm, but that it is produced by the host under stimulation. However that may be, the production of anti-enzymes is not peculiar to the parasite, and at the most, as was said at the beginning of this discussion, it is only making special use of a general property of living tissue.

The second aspect of the chemical relationship is that of the reaction of the host to the parasite, which leads, it is to be presumed, to the host-restriction of the parasite. Sometimes only a single species of host seems possible; thus all attempts to infect chimpanzees with *Plasmodium malariæ* have failed; human *P. vivax* transferred to chimpanzees disappeared and apparently gave no infection, but that it was present was proved because another man could be infected from the ape. At the other extreme adults of *Trichinella spiralis* have been found naturally in man, pig, fox, cat, and both species of rat, and experimentally all mammals that have been tried have taken the infection, and although birds are not susceptible, salamanders are if they are kept at 30° C. Some degree of restriction between these extremes is the common state. It is often found that, while transference from one host to another is impossible, parasites of morphologically identical

form occur in the second host. Thus the three species of *Plasmodium* found in man are all paralleled in the higher apes ; *Entamœba histolytica* of man and *E. ranarum* of frogs are morphologically indistinguishable, and, except for the size of the labial teeth, the same is probably true of *Ascaris lumbricoides* and *A. suillæ*. Whether such forms should be classed as separate species is a question beyond the scope of this chapter, but it is well to remember that man, living in a visual world, is apt to overvalue visual stimuli. He cannot consciously distinguish *E. histolytica* and *E. ranarum*, because he tries to do so by his eyes alone ; the epithelium of his intestine can, however, tell the difference between them. Other animals can make a similar distinction between the morphologically identical *Trypanosoma equiperdum* living in the connective tissue of horses and transmitted during coitus, and *T. evansi* living in blood and carried by a tabanid vector. We may safely assume that the differences between all these forms, whether we call them biological races or distinct species, are fundamentally chemical. Such biological races, though commoner amongst parasites, are not confined to them, being also found, for instance, amongst phytophagous insects.

13

EARTHWORMS AND OTHER ANNELIDS

LUMBRICUS TERRESTRIS

Earthworms are found in the soil in almost all parts of England, in rich soils making up more than half the total weight of living

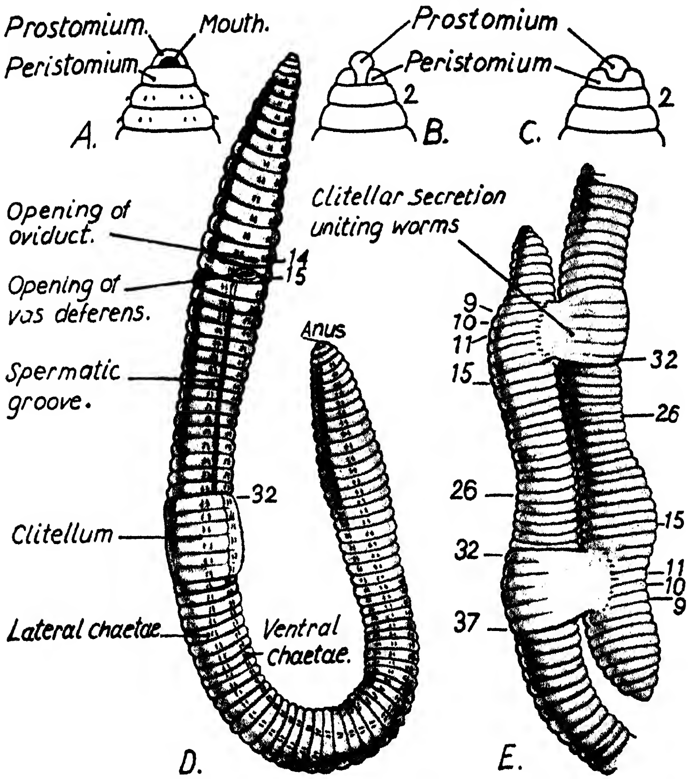


FIG. 13.1.—*A*, The first three segments of an earthworm, *Lumbricus terrestris*, ventral; *B*, the same, dorsal showing the epilobous condition; *C*, the first three segments of *Allolobophora*, dorsal (tanylobous); *D*, *Lumbricus terrestris*, ventrolateral; *E* (after Grove), worms in coition. In *B–E* the numbers refer to the segments.

matter. There are several species in some half-dozen genera, and their distribution is complicated, depending on the nature of the soil, its acidity, its agricultural history, the organic matter that it contains, and its geographical situation. In general there are

fewer species and fewer individuals in the more acid soils, though some of the smaller species can tolerate a pH of 3.5. The species differ not only morphologically but in their habits. Thus while all burrow by eating the soil, only *Allolobophora longa* and *A. nocturna* (in this country) void their fæces on the surface, so making the familiar worm casts. *Lumbricus terrestris* appears to be alone in the habit of stretching the front part of the body out of the hole while leaving the rear portion anchored within it. Some take leaves and small stones into their holes. The conditions under which they leave their burrows and crawl on the surface seem to be unknown, but they certainly do this less in dry weather and in the daytime than after rain and at night. When the ground is hard, whether from frost or sun, they burrow deep, *Lumbricus terrestris* going down sometimes to six feet.

Charles Darwin was the first to stress the great importance of earthworms to agriculture. They mix the soil, break down its particles, open it to the action of air and water, and digest its raw humus. In fields with a high population of the cast-forming species as much as 25 tons per acre per annum may be brought to the surface.

EXTERNAL FEATURES

One of the commoner English earthworms is *Lumbricus terrestris* (Fig. 13.1). The body of this animal is roughly cylindrical, but pointed in front and flattened behind. It reaches a length of seven inches. There is no distinct head, but a lobe known as the prostomium overhangs the mouth, which is a crescentic opening on the lower side of the front end. The body is divided into a series of rings, the segments, and at the hinder end is the terminal anus. The first segment is the peristomium and the mouth lies between it and the prostomium. On the dorsal side, the latter projects across the peristomium. There are about 150 segments, but the number probably increases slightly throughout life. (In the related *Allolobophora* the prostomium reaches only half-way across the peristomium, and the common *A. chlorotica* has about 110 segments.) At about one-third of the length of the body from its front end, in segments 32–37 inclusive, a glandular thickening of the epidermis lies athwart the back like a saddle; it is known as the clitellum. The colour of the worm ranges from brown to purplish, but is somewhat paler below; *A. chlorotica* has a

greenish variety which is especially common in grassland. The skin is covered with an iridescent cuticle of collagen secreted by the underlying cells. In every somite except the first and the last there are eight bristles, the chætæ or setæ (Fig. 13.2) in two pairs on each side, a lateral pair, slightly above the middle of the side, and a ventral pair between the lateral and the mid-ventral line. The chætæ can be felt with the fingers; they are made of chitin, which is effectively an aminocellulose, and are embedded in sacs of the epidermis, by which they are secreted, and to these sacs are attached muscles, by which they can be moved. The chætæ, as we shall see later, assist in locomotion. The ventral chætæ of the clitellum, of the twenty-sixth, and of the tenth to the fifteenth segments, are straighter and more slender than those of other segments, which are stout and somewhat bent. This modification is in connection with the use of the chætæ of the twenty-sixth segment during coition, and of the other straight chætæ during the formation of the cocoon in which the eggs are laid.

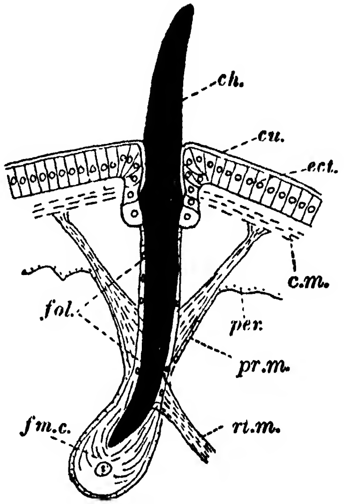


FIG. 13.2.—A diagram of a chæta of the earthworm and the structures connected with it.—From Potts, after Stephenson.

c.m., Circular muscle of body-wall; *ch.*, chæta; *cu.*, cuticle; *ect.*, ectoderm; *fol.*, follicle; *fm.c.*, formative cell of chæta; *per.*, peritoneum; *pr.m.*, protractor, and *rt.m.*, retractor muscles of chæta.

EXTERNAL OPENINGS

A number of internal organs open separately upon the surface of the body. We have already mentioned the mouth and anus. The openings of the vasa deferentia are a pair of slits with swollen lips found on the under side of the body in segment 15. In front of them, in somite 14, are the two small openings of the oviducts. The spermathecal pores are two pairs of small, round openings in the grooves between segments 9–10 and 10–11 at the level of the lateral chætæ, but *Allolobophora* may have three pairs. The nephridiopores are openings which lead from the excretory tubes or nephridia. They are found, as a pair of minute pores in front of the ventral chætæ, in each somite except the first

three and the last. The dorsal pores are small, round openings on the mid-dorsal line in the grooves between the segments. The first is behind the eighth segment, and there is one in each subsequent groove. They open into the body cavity, the fluid in which oozes out through them and moistens the surface of the body, mingling with the slime secreted by the unicellular glands of the skin. As this fluid contains amœboid cells which attack bacteria and other small parasites, it is a valuable defence to the worm against such enemies, which are numerous in the soil.

BODY-WALL

The body of the worm may be said to consist of two tubes, one within the other (Fig. 13.3). The inner tube is the gut, the outer the body-wall. Between the two lies the cœlom or body cavity, divided into compartments by a series of septa, which reach from the gut to the body-wall, where they are attached opposite the grooves on the surface of the body. The compartments communicate by numerous openings in the septa. The cœlom contains a fluid, and in this float the leucocytes already mentioned, by which small parasites are surrounded and destroyed, both within and without the body. The body-wall is covered by a cuticle. Under this lies the epidermis, an epithelium consisting of columnar cells, many of which are glandular or sensory, with small cells between their bases. The cuticle is composed of hardened protein and is perforated by a pore above each gland cell. The epidermis of the clitellum consists of several layers of gland cells. Below the epidermis is a circular layer of muscle, consisting of unstriped fibres running around the body, and below this again lies a much thicker longitudinal layer of muscle, composed of similar fibres running along the body and placed in rows which stand at right angles to the surface, supported by connective tissue. On the inner side of the longitudinal muscle is the cœlomic epithelium, which is here a layer of pavement cells lining the body cavity.

NUTRITION

The alimentary canal is straight. It begins with a short, wide, thin-walled mouth or buccal cavity in the first three somites, which leads to a muscular region known as the pharynx. This lies in front of the septum between the fifth and sixth somites, but

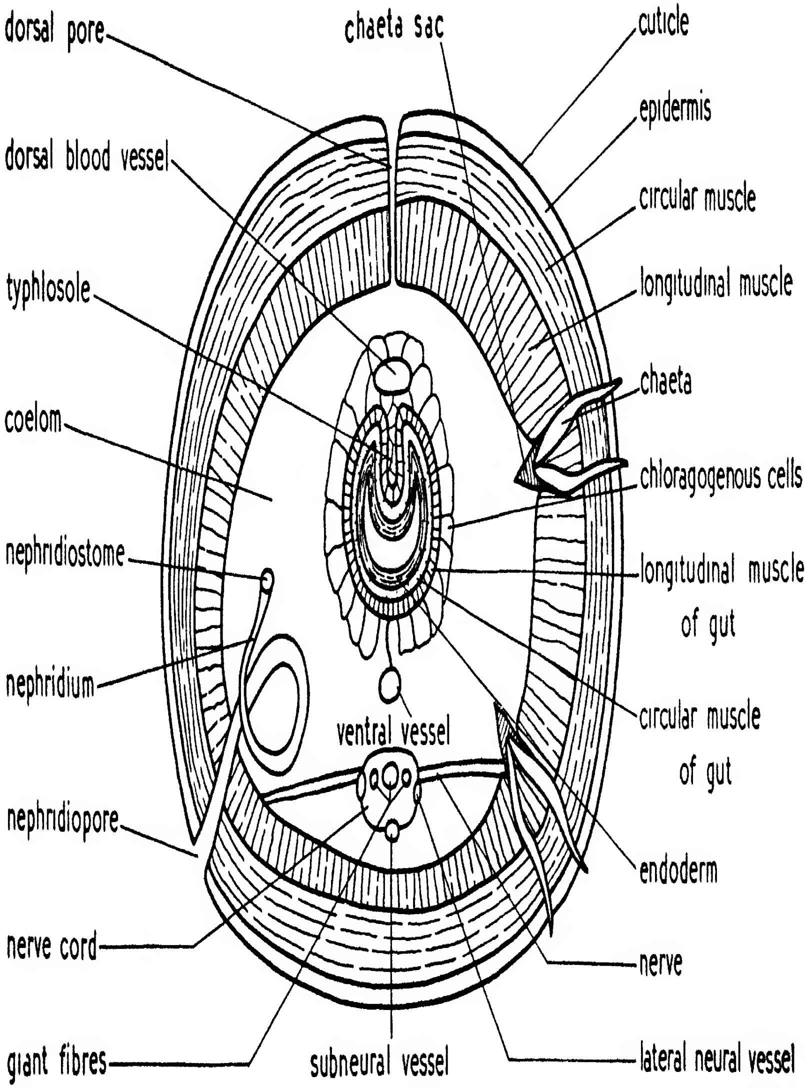


FIG. 13.3 — A diagrammatic transverse section of an earthworm in the intestinal region A nephridium is shown on the left; chæta on the right The dorsal pore is in a different plane from both of these

pushes that septum backwards as far as the seventh. When the worm is swallowing soil the pharynx is everted to a length of a few millimetres. Its dorsal wall is thickened by the presence of

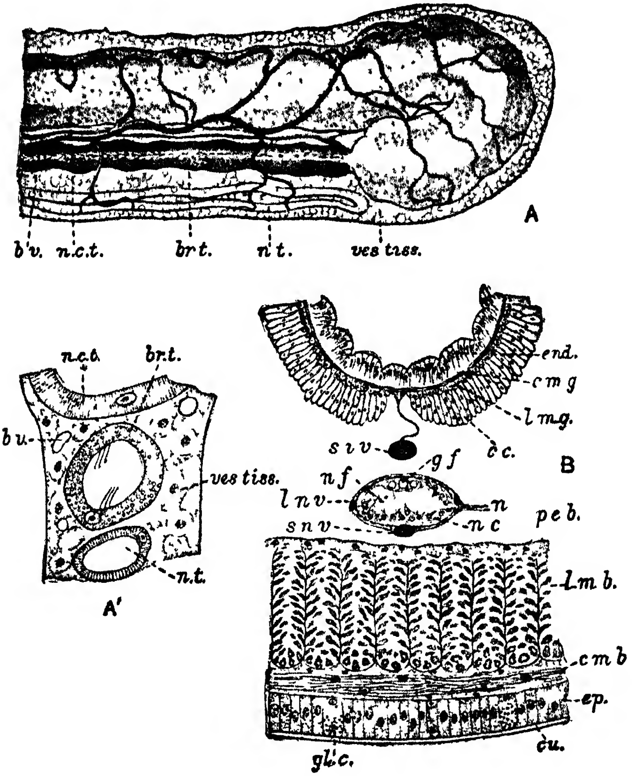


FIG 13 4 —Histology of the earthworm

A, The end of the first hank of the nephridium , *A* , part of a section of the same , *B*, part of a transverse section of the body

br t Brown, ciliated tube , *b v* blood vessel *c c* , chloragogenous cells *c m b* , circular muscle of body-wall *c m g* circular muscle of gut *cu* , cuticle *ep* epidermis , *end* endoderm *g f* , giant fibres *gl c* gland cell in the epidermis *l m b* longitudinal muscle of body wall *l m g* longitudinal muscle of gut *l n v* , lateral neural vessel *n* nerves *n c* , nerve cord *n c t* , glandular non ciliated tube *n f* , nerve fibres , *n t* , narrow tube, ciliated in parts *p e b* , peritoneal epithelium of body wall *s i v* subintestinal blood vessel , *s n v* , subneural blood vessel , *ves tiss* , connective tissue with vesicular cells and blood vessels

a number of glands, whose secretion, containing mucin and a ferment which digests proteins, is poured over vegetable tissues while the animal is feeding upon them. Numerous strands of muscle run from it to the body-wall. Behind it lies the œsophagus, a straight, narrow, thin-walled tube, which extends to the fourteenth segment. In the eleventh segment it bears at the sides

a pair of œsophageal pouches, and in the twelfth two pairs of œsophageal or lime glands. These contain large cells which secrete calcium carbonate and pass it through the pouches into the œsophagus. In the fifteenth and sixteenth segments the œsophagus expands into a large, thin-walled crop, which in turn communicates behind with the gizzard, another swelling, with thick muscular walls and a chitinous lining, in segments 17 and 18. From the gizzard to the anus runs a wide, thin-walled tube known as the intestine. The intestine is narrowed where it passes through the septa, and its dorsal wall is infolded to form a longitudinal ridge known as the typhlosole. The gut is lined with a layer of columnar epithelium, outside which are thin longitudinal and circular muscular layers, covered by the cœlomic epithelium, which here consists of the chloragogenous cells. These cells, which also fill the typhlosole, are large and contain yellow granules of a substance which is possibly a phospholipid. They fall off into the cœlomic fluid, and there break up and set free their granules, which are taken up by amœbocytes. It is said that these may go to the exterior, but as the granules contain only four per cent. of nitrogen they cannot be an important excretory product. There are also amœboid yellow cells which take up excreta in the blood, pass into the gut, and are voided with the fæces.

Food swallowed in the course of burrowing is passed along the œsophagus, stored in the crop, ground up in the gizzard with the aid of small stones which have been swallowed, and in the intestine first digested by juices secreted from the epithelium, and then absorbed, for which processes the surface is increased by the presence of the typhlosole. The contractions which cause the passage of the food are alternately started through the nerves to the pharynx and inhibited through the plexuses in the septa. From the anus fæces and undigested soil are passed out as the familiar worm casts (in *Allolobophora*) or in the burrows below the surface. The function of the œsophageal glands is probably the excreting of the calcareous matter which is very plentiful in the dead leaves of which the food is largely composed. Possibly their secretion is also of importance in removing carbon dioxide in the form of calcium carbonate. They are characteristic only of those species of worm which are large and live in a relatively dry environment.

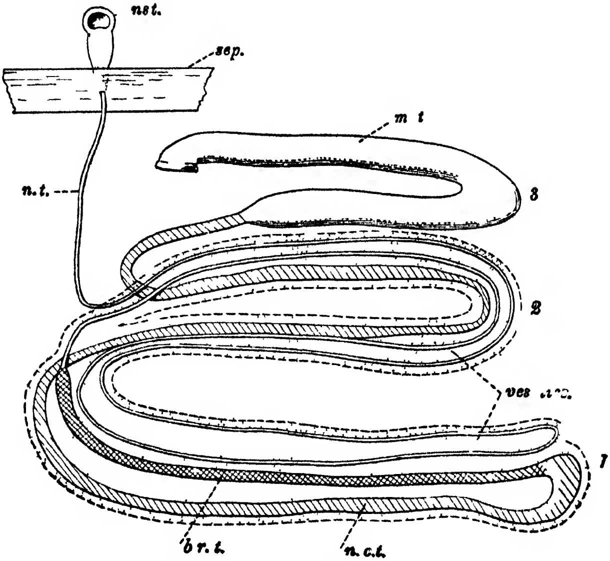


FIG 13 5 – A diagram of a nephridium of the earthworm

br t Brown ciliated tube, *m t* muscular tube, *n c t*, glandular, non ciliated tube, *n t* narrow tube, ciliated in parts, *nst*, nephrostome, *sep* septum, *ves tiss*, connective tissue with vesicular cells and blood vessels 1, 2, 3, the three hanks of the tube

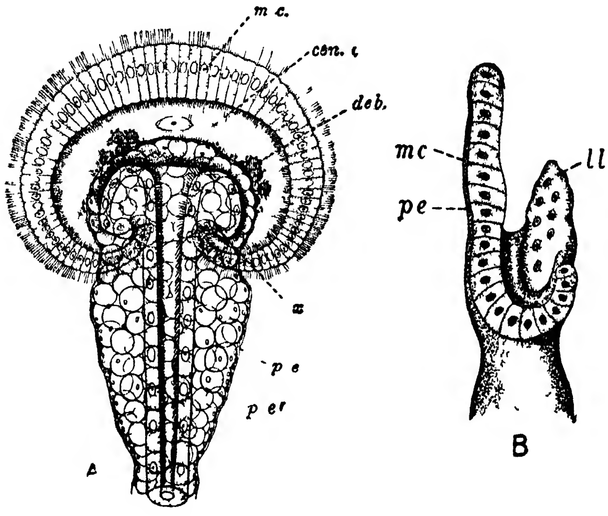


FIG 13 6—The nephridiostome or funnel of a nephridium of the earthworm *A*, Seen from in front as a transparent object, *B*, in side view, opaque semi diagrammatic, and without its cilia

cen c, Central cell *deb* debris of cœlomic corpuscles and excretory granules which is probably not able to enter the funnel *l l* lower lip of opening *m c* marginal cells *p e*, superficial layer of the peritoneal epithelium *p e'* thickened deeper layer of the same *x*, point at which the marginal cells join the lining of the tube which turns over round the opening

EXCRETION

Besides the yellow cells of the intestine, the earthworm has excretory organs which, like those of vertebrates, consist of tubes with walls that are glandular and excretory and richly supplied with blood vessels; but the tubes, instead of being collected into compact kidneys, are distributed along the body, one pair to each segment, except the first three and the last which have none. Each tube or nephridium is thrown into loops, bound together by connective tissue containing blood vessels. The inner end of the nephridium (Figs. 13.5, 13.6) is a flattened, kidney-shaped funnel or nephridiostome hanging from the front side of a septum near the nerve cord. The nephridiostome has an overhanging lip which consists of a large crescentic central cell with a row of marginal cells around it. This lip is ciliated. The lower lip is not ciliated. From the funnel there leads a narrow tube, ciliated on its sides. This passes through the septum to the main part of the nephridium, which lies behind the septum, in the cœlom of the next somite, opening to the exterior by the nephridiopore in that somite. The narrow part of the tube is long and winding and loses its cilia in places. It is followed by a wider, short, brown region, ciliated throughout, this by a still wider tube which is not ciliated, and finally a short, very wide, muscular tube leads to the nephridiopore. The whole tube, except the muscular region, is formed of hollow cells shaped like drain-pipes and lying end to end. The middle part of the nephridium stores excretory granules probably throughout life, and a fluid is also driven to the exterior, being liberated by the opening of the nephridiopore once every three days. The chief excretory constituents of this urine are urea and ammonia. These are probably derived from both blood and cœlomic fluid, and there appears to be filtration, reabsorption and secretion, much as in the vertebrate kidney (p. 453).

BLOOD VESSELS

Earthworms have no special respiratory organs, but an interchange of gases between the air and the blood takes place in the skin, which is richly supplied with vessels.

The blood of an earthworm is red owing to the presence in it of a substance generally called hæmoglobin, although it is different in composition from the pigment of the same name in vertebrates

This hæmoglobin is in solution, not in corpuscles. Colourless corpuscles are also present. The blood-vascular system is very complicated. Its main outlines are as follows (Figs. 13.7–13.9). A large dorsal vessel runs the whole length of the body from the

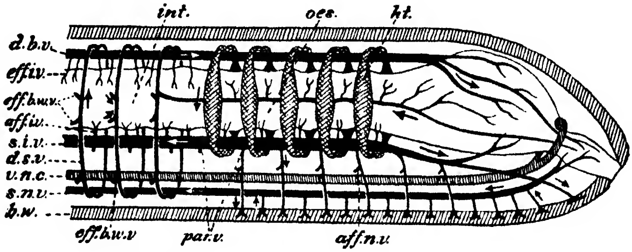


FIG. 13.7.—A diagram of the blood-vascular system of the earthworm.

aff.i.v., Afferent vessels of the intestine; *aff.n.v.*, afferent vessels of the nephridia; *b.w.*, body-wall; *d.b.v.*, dorsal blood vessel; *d.s.v.*, dorso-subneural vessel; *eff.b.w.v.*, efferent vessel from body-wall; *eff.i.v.*, efferent vessel from intestinal wall; *ht.*, pseudo-hearts; *int.*, intestine; *œs.*, œsophagus; *par.v.*, parietal vessel; *s.i.v.*, subintestinal vessel; *s.n.v.*, subneural vessel; *v.n.c.*, ventral nerve cord.

A simpler form of this diagram will be found below.

hinder end to the pharynx. It is contractile and its walls contain muscle fibres, and in it the blood is driven forwards. It receives blood by many small vessels from the intestine and by two larger

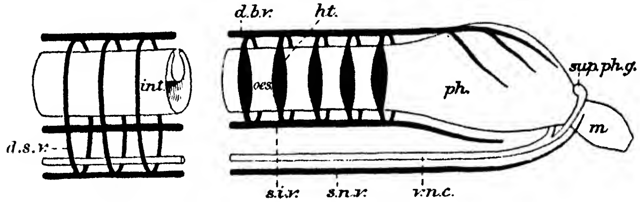


FIG. 13.8.—A diagram of the principal blood vessels of the earthworm.

d.b.v., dorsal blood vessel; *d.s.v.*, dorso-subneural vessel; *ht.*, one of the 'hearts'; *int.*, intestine; *m.*, mouth; *œs.*, œsophagus; *ph.*, pharynx; *sup.ph.g.*, suprapharyngeal ganglion; *s.i.v.*, subintestinal vessel; *s.n.v.*, subneural vessel; *v.n.c.*, ventral nerve cord.

vessels in the tenth segment from the œsophagus, and ends in front by breaking up into branches which supply the pharynx. In each of the segments 7–11 it gives off a pair of large contractile vessels or pseudo-hearts. These encircle the œsophagus and join a ventral or subintestinal vessel which hangs by a mesentery below the gut. In the pseudo-hearts the blood flows downwards from the dorsal to the ventral vessel, and in the latter it flows backwards and forwards from the region of the hearts. From the ventral vessel the blood passes by a series of small vessels to the intestine, and by parietal vessels to the nephridia and to the body-wall. From these organs it is returned along various paths to

the dorsal vessel. Among the subsidiary vessels are a subneural and two lateral neural vessels, in which the blood flows backwards, and dorso-subneural vessels, a pair in each segment of the intestinal region of the body, which carry blood to the dorsal vessel from the subneural vessel, the nephridia, and the body-wall. The main blood vessels of the earthworm cannot be distinguished into arteries and veins, but their ends are joined by capillaries. The dorsal vessel and the pseudo-hearts are provided with valves which keep the blood flowing in the proper direction.

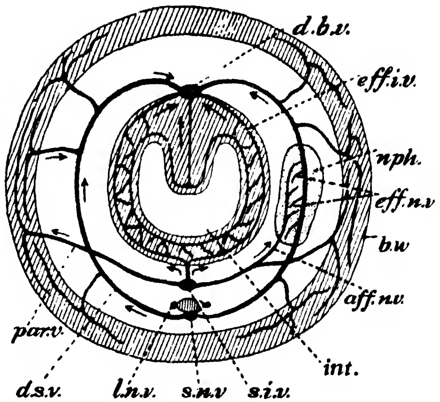


FIG. 13.9.—A diagram of a transverse section of the earthworm in the intestinal region to show the arrangement of the blood vessels.

eff.n.v., Efferent vessel from nephridium; *l.n.v.*, lateral neural vessel; *nph.*, nephridium; other lettering as in Fig. 13.7.

NERVOUS SYSTEM

The earthworm has a well-developed central nervous system (Fig. 13.10), which consists of (1) a pair of suprapharyngeal ganglia, rounded bodies lying above the mouth, and sometimes known together as the brain, (2) two slender circumpharyngeal commissures running from these round the pharynx, and (3) a ventral nerve cord which starts from the commissures between the third and fourth somites and runs the whole length of the body in the cœlom below the gut, swelling into a ganglion in each somite. The first of these ganglia is bilobed and is known as the subpharyngeal ganglion. Nerves are given off to the prostomium from the suprapharyngeal ganglia, and to the first two somites from the commissures, and the ventral cord gives off in each somite three pairs of nerves which run upwards as girdles in the body-wall, giving off branches as they go. The alimentary canal receives nerves from the circumpharyngeal commissures and fibres from plexuses in the septa. Though the ventral cord appears to be single, it is really double, and can be seen in transverse sections to be rather imperfectly divided into right and left halves by connective tissue. Transverse sections also show that

the middle and upper parts of the cord consist of fine, chiefly longitudinal, nerve fibres, and the lower and outer parts contain nerve cells. Above the mass of fine fibres are three longitudinal bundles of such fibres, each bundle being enclosed in a sheath and known as a giant fibre. Nerve cells are more numerous in, but not confined to, the ganglia. The nerves consist of afferent fibres, which start from sense cells in the epidermis and muscles (Fig. 13.11) and carry impulses to the central nervous system, and of efferent fibres, which start from nerve cells in the ganglia and end against muscle and other cells, to which they convey impulses.

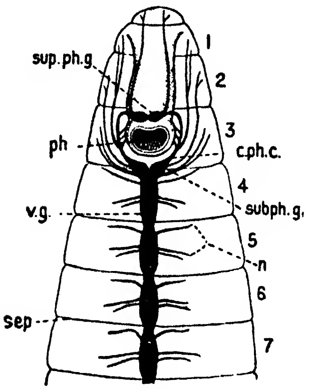


FIG. 13.10.—A diagram of the forepart of the nervous system of the earthworm.

c.ph.c., Circumpharyngeal commissure ; *n.*, nerves ; *ph.*, pharynx cut through ; *sep.*, septa ; *subph.g.*, subpharyngeal ganglia ; *sup.ph.g.*, suprapharyngeal ganglia ; *v.g.*, ganglia of ventral cord 1–7, somites.

MOVEMENT

On the surface, worms move by means of a peristaltic contraction of the muscles of the body-wall. Two series of waves of contraction, one of the longitudinal and one of the circular muscles, pass along the body from the anterior end ; the waves of the two series are out of phase with each other, contraction in one set of muscles in a particular segment being accompanied by relaxation of the other. If a worm which is lying quiescent, in moderately contracted state, starts moving, the following things happen in order. The circular muscles of the first segment contract, making it longer and narrower ; then the second segment behaves similarly, and the third and fourth, and so on, so that the anterior part of the body is elongated. When this contraction wave has reached about a third of the way along the body, the longitudinal muscles of the first segment begin to contract ; they are followed by those of the following segments, and the second type of waves has begun. As each wave dies out it is succeeded by another. These waves by themselves would not lead to locomotion at all, but merely to successive extensions and withdrawals of the two ends of the body, the mid-point or centre of gravity remaining stationary ; something like this may

sometimes be seen when a worm tries to move on a wet glass plate. To translate the waves into progression there must be some greater resistance to movement backwards than there is to movement forwards. This differential resistance is achieved in three ways. It can often be seen that the part of the body which is moving forward is raised off the ground; this eliminates surface friction. In ordinary slow crawling the head is lifted and thrust forward; the contraction wave dies out about half-way along the body, and when the anterior end shortens the tail part is raised slightly and dragged forwards. Secondly, the chætæ play some, though probably a minor, part in movement. When the longitudinal muscles contract the chætæ are generally simultaneously extended. As those of the first dozen or so segments point backwards they will resist backward movement more than forward; those of the middle part of the body stand out radially, or slightly irregularly, so that they will resist forward and backward movement equally. Those of the posterior segments point strongly forwards, and if erected would tend to make the worm move backwards; as has been said, the contraction waves do not normally reach this part of the body, and so the chætæ are not extended. Finally, and probably most important, the anterior end of the body acts as a sucker. In some worms the prostomium and peristomium, in others the everted pharynx, are pressed against the surface, and the prostomium is then withdrawn;

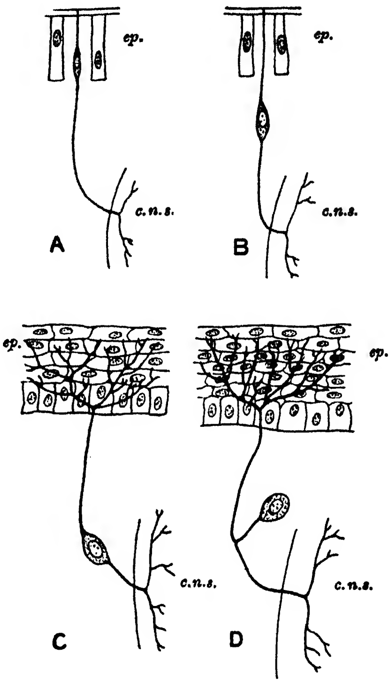


FIG. 13.11.—A diagram showing the mode of ending of the sensory nerve fibres in the epidermis of the earthworm and the relation of this type to that which is found in some other animals.

See also Fig. 26.29.

A, The arrangement found in the earthworm; *B*, that of the worm *Nereis*; *C*, that of a fish; *D*, that of a frog or man.
c.n.s., Ending of the neuron in the central nervous system; *ep.*, ending in the epidermis.

when this happens the anterior end is anchored, and any shortening of the body must pull the animal's centre of gravity forward. By this means a worm can crawl up a vertical plate of glass or metal (Fig. 13.12).

Burrowing takes place by two methods. If, when the anterior end of the body is elongated, it comes into any small crevice, instead of contracting, as it normally would do on contact, it continues to press in. Then when the wave of longitudinal contraction starts, the anterior segments expand radially and press against the sides of the crevice so that they cannot be withdrawn. By this means, which is akin to the technique of chimney-climbing known as backing-up, a worm can move through a glass tube, and it is probable that much of its burrowing is done in this way (Fig. 13.13). In loose soil a more or less cylindrical burrow will be formed by the pressure of the segments against the side of the crack into which the worm puts its snout. Sometimes on contact with soil the worm extends its pharynx and sucks in a mouthful ; repeated sucking creates a hollow in which the backing-up process can be used. A little soil is sometimes swallowed without protrusion of the pharynx. It is probable that burrowing in firm soil is impossible unless the worm eats its way through (Fig. 13.14).

When a worm is strongly stimulated it may move backwards by a reversal of the normal waves. It is probable that this reaction seldom occurs on the surface in nature, but it is important in preventing the worm from being withdrawn from its burrow. The longitudinal muscles of the posterior segments are strongly contracted, with extrusion of their chætæ. As has been said, these project forwards, and if this part of the worm is below ground they will be driven into the soil. If the anterior end is seized and pulled, as it often is under these circumstances by a thrush, either the chætæ, or the soil, or the worm, must break, and usually it is the worm.

The co-ordination of the contraction waves is carried out in part mechanically because the stretching of the muscles causes them to contract, and in part by the nervous system. The contraction of circular or longitudinal muscles in a somite causes, through an impulse sent along the ventral cord, the contraction of the corresponding muscles in the somite behind. Further, in each somite the contraction of the circular musculature sends, by afferent and efferent fibres, through the

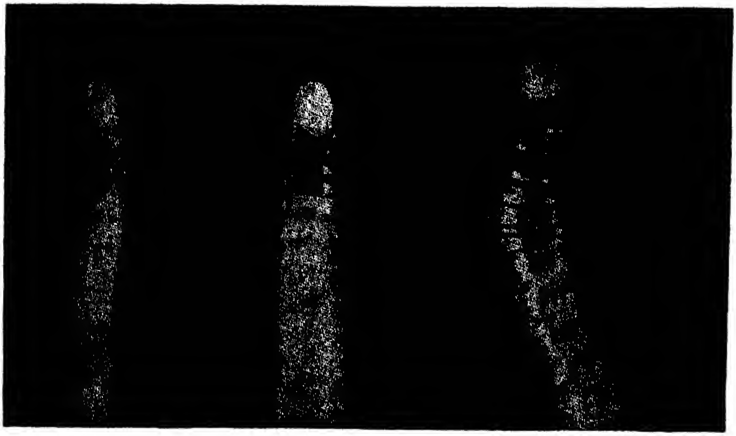


Fig. 13 12.—An earthworm, *Eisenia fœtida*, climbing up a vertical glass plate. × 3 5 The three photographs show stages in the eversion of the pharynx —From Roots and Phillips, *Med. biol Ill.*, 1960. 10, 28.

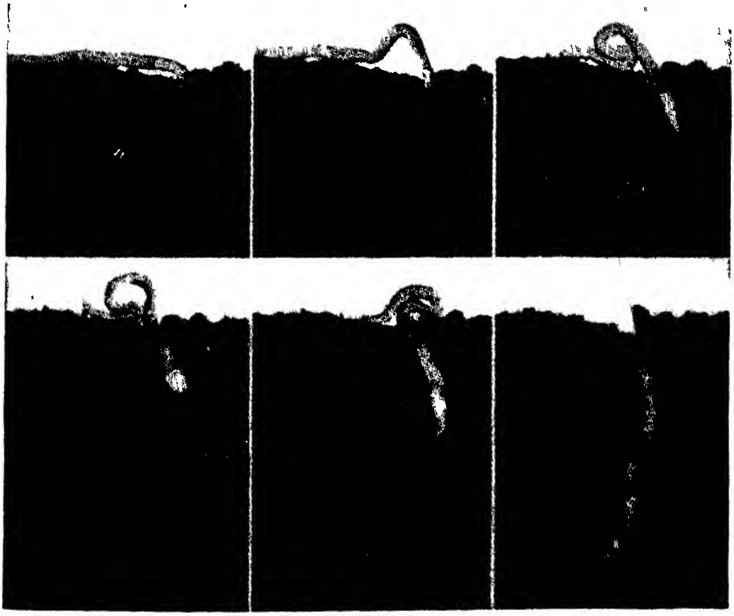


Fig. 13.13 —*Lumbricus terrestris* burrowing by backing-up × 0.5.—From Roots and Phillips, *Med. biol. Ill.*, 1960. 10, 28.

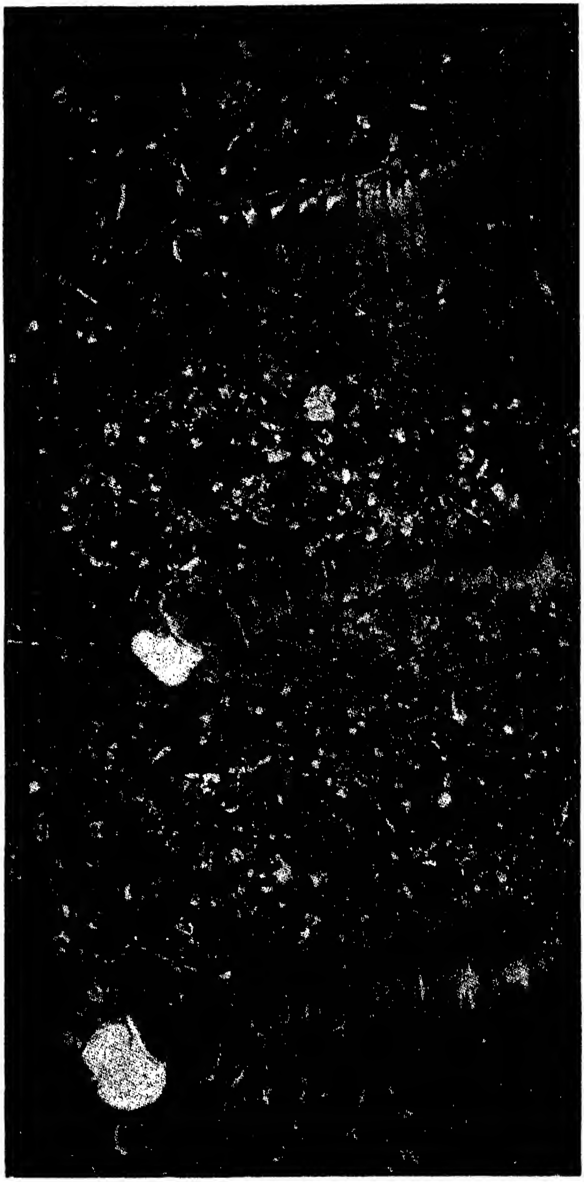


FIG. 13.14.—Stages in the eversion of the pharynx of a burrowing *Lumbricus terrestris*. × 3.5.—From Roots and Phillips, *Med. biol. Ill.*, 1960, 10, 28.

ganglion, impulses which relax the longitudinal musculature; and similarly the longitudinal muscles in contracting relax the circular. Rapid contraction is co-ordinated by nervous impulses which travel in the giant fibres, forwards in the laterals, and from head to tail in the median fibre.

SENSE ORGANS

An earthworm has no well-developed organs of sense, but certain of the columnar cells of the epidermis are rod-shaped and prolonged at their inner ends into fibres, which run in the

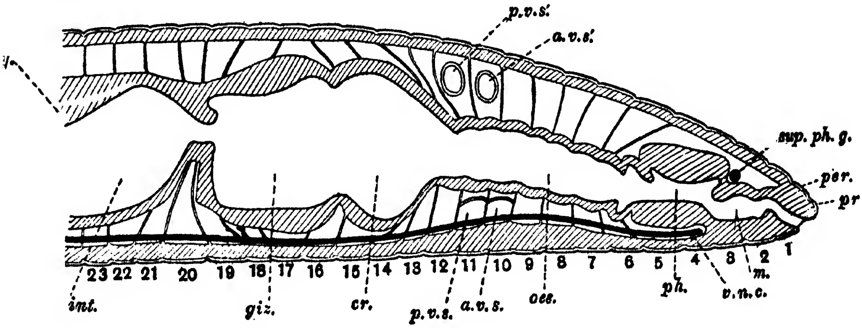


FIG. 13.15.—A diagram of a longitudinal section of an earthworm.

a.v.s., Anterior vesicula seminalis; *a.v.s'.*, posterior lateral horn of the same overhanging the œsophagus; *cr.*, crop; *giz.*, gizzard; *int.*, intestine, *m.*, mouth; *œs.*, œsophagus; *p.v.s.*, posterior vesicula seminalis; *p.v.s'.*, horn of the same overhanging the œsophagus; *per.*, peristomium; *ph.*, pharynx; *pr.*, prostomium; *sup.ph.g.*, suprapharyngeal ganglion; *ty.*, typhlosole; *v.n.c.*, ventral nerve cord; 1–23, segments. The blood vessels are omitted.

nervous system. These are sense cells, and in the forepart of the body some of them are collected into groups, which are rudimentary sense organs (Fig. 13.15). There are also sense cells which contain a refractive body and are probably affected by light. Experiment shows that the worms are sensitive to light and to vibrations of the ground, and can smell, but gives no evidence of a sense of hearing.

REPRODUCTION

Earthworms are hermaphrodite, every individual having a complete set of organs of each sex (Figs. 13.16, 13.26). The female organs include the ovaries, oviducts, and spermathecæ. The ovaries are two small, pear-shaped bodies hanging into the cœlom of the thirteenth segment from the septum in front of it. Each ovary

is a local thickening of the cœlomic epithelium, and is just visible to the naked eye, as a whitish spot (Fig. 13.17). The broad end of the pear is attached to the septum and contains a fused mass of unripe ova. Ova fall from the stalk into the cœlom and are taken up by the oviducts, which lead by wide funnels from the cœlom in the thirteenth somite, pass through the septum behind, and open to the exterior in the fourteenth. In the latter somite, each bears a swelling, the receptaculum ovorum or egg sac, in

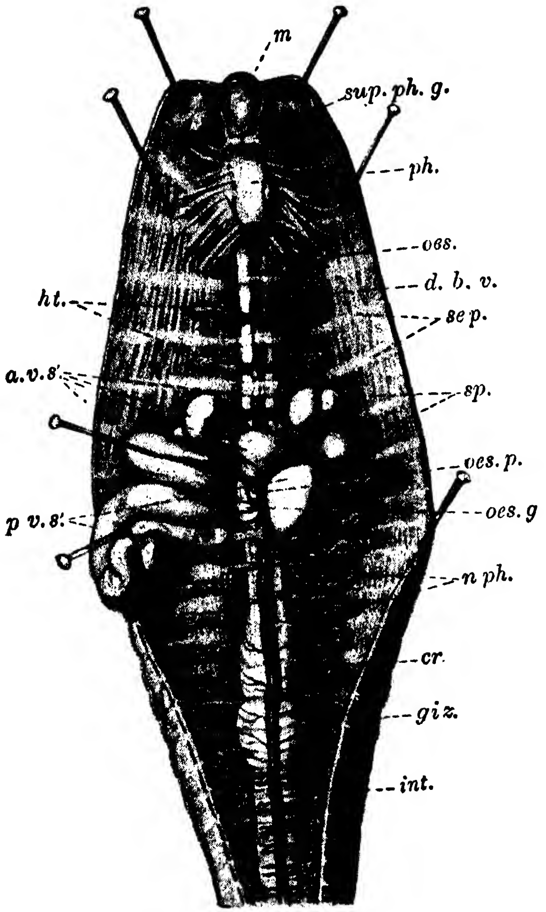


FIG. 13.16.—An earthworm (*L. terrestris*), dissected from above.

a.v.s'., Horns of the anterior vesicula seminalis; *cr.*, crop; *d.b.v.*, dorsal blood vessel; *giz.*, gizzard; *ht.*, hearts; *int.*, intestine; *m.*, mouth; *nph.*, nephridia; *œs.*, œsophagus; *œs.g.*, œsophageal glands; *œs.p.*, œsophageal pouch; *p.v.s'.*, horns of the posterior vesicula seminalis; *ph.*, pharynx; *sep.*, septa *sp.*, spermathecæ; *sup.ph.g.*, suprapharyngeal ganglia.

which the eggs are stored and maturation divisions take place. The spermathecæ are two pairs of small, round sacs which lie in the ninth and tenth somites and open in the grooves behind them. Their function is to receive sperm from another worm. The male organs consist of testes, vesiculæ seminales (seminal vesicles), and vasa deferentia. These testes are two pairs of small, flat, finger-lobed bodies attached to the hinder side of the septa in front of segments 10 and 11. Like the ovaries, to which they correspond in position, they are local thickenings of the cœlomic epithelium. The testes bud off cells known as sperm-mother-cells, which give rise to spermatozoa in the seminal vesicles. The latter are large sacs, formed by the walling-off of parts of the cœlom, which enclose the testes. Each consists of a median part and lateral horns. The anterior seminal vesicle, in segment 10 has four lateral horns, two in front and two behind, which push out the septa and bulge into the ninth and eleventh segments. The posterior seminal vesicle in segment 11, has only two such horns, which project into the twelfth segment. Each sperm-mother-cell forms by multiple fission, in the course of which the usual reduction division takes place, a mulberry-like mass (Fig. 13.18), consisting of little cells attached to a central mass of residual protoplasm known as the cytophore, by which they are nourished. The little cells become pear-shaped, with the broad ends on the cytophore, gradually increase in length, and change their shape till the mulberry has become a tuft of threads, each thread being a spermatozoon with a very slender head. Finally the spermatozoa break loose. In the median part of each seminal vesicle, directly behind the testes, is a pair of large ciliated funnels with folded walls, known as sperm rosettes. These funnels lead into the vasa efferentia, of which the two on each side join and pass back as a vas deferens to open on somite 15. The cilia of the rosettes draw the ripe sperm into the ducts.

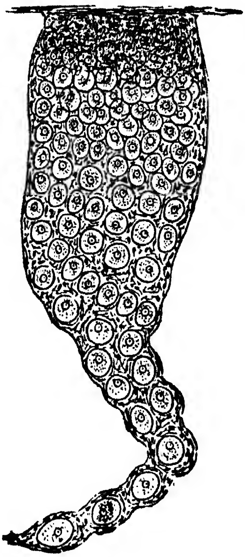


FIG. 13.17.—One of the ovaries of an earthworm.

Copulation (Fig. 13.1) takes place at any time from spring to autumn in warm, damp weather, with a maximum frequency in

the hot weather of summer. Two worms stretch themselves out of their burrows and place their ventral sides together with the heads pointing in opposite directions, their bodies being held together by a substance secreted from the clitella, and by the

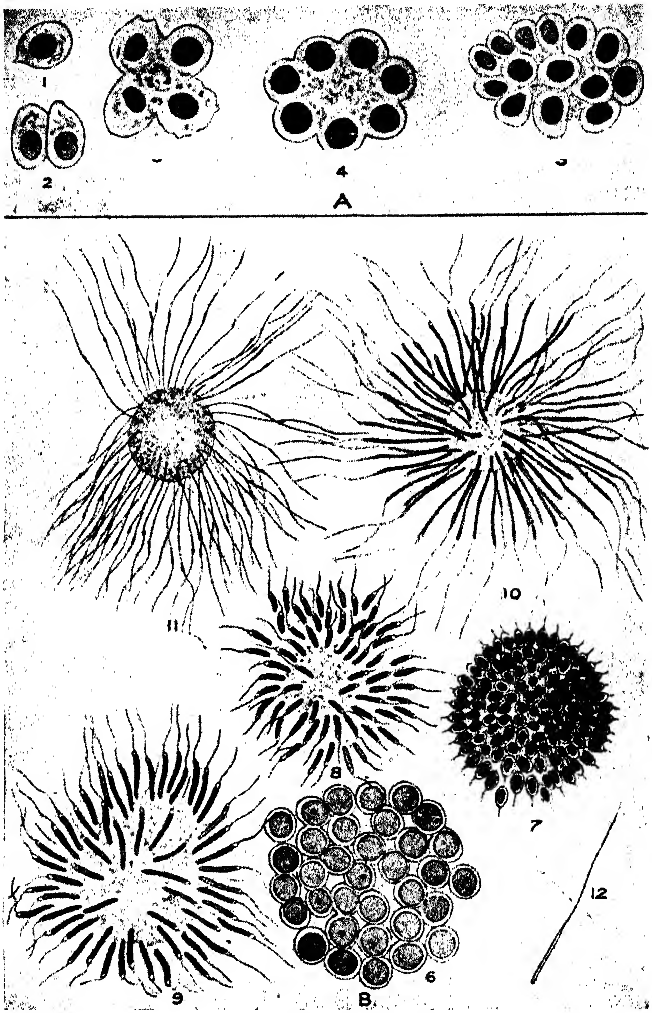


FIG. 13.18.—The development of the spermatozoa of the earthworm.

A, Stages from the vesicula seminalis of a young worm ; *B*, from that of an older worm.
C, Sperm-mother-cell ; 2–7, stages in the division to form spermatozoa ; 7–11, shaping of the spermatozoa which are still adherent to the mass of residual protoplasm (cytophore) 12, a ripe spermatozoon unstained. The head in 12 is represented rather too broad.
The dark bodies are the nuclei, stained.

chætæ, which stab into the body-wall of the partner. They remain like this for two or three hours, and sperms are passed from the vas deferens of each worm, along a temporary seminal groove, into the spermathecæ of the other. Some time after the worms have separated the eggs are laid in a cocoon, which, secreted by the clitellum as a broad band round the body, is passed forwards over the head. The cocoon contains a nutrient fluid. While it is still on the clitellum eggs are passed back to it along a temporary groove from the oviducal opening, and as it passes the spermathecal openings, semen received from another worm is squeezed into it and fertilisation takes place immediately. In passing over the head the ends of the elastic cocoon close, and it becomes a small, lemon-shaped body, which is left in the earth. Each cocoon contains eight to sixteen ova, which are fertilised in it, but usually only one completes development, a process which takes several weeks. The development of the earthworm is referred to on p. 679.

REGENERATION

Many earthworms have an extensive power of regeneration, which depends on a hormone secreted by the central nervous system. If the body be cut in half, the head end will grow a new tail, and the tail end, though more slowly, a new head. It appears that, of the two common species described above, *Allolobophora chlorotica* does regenerate, but *Lumbricus terrestris* does not.

NEREIS CULTRIFERA

The earthworm has a burrowing habit and a vegetarian diet. Many marine worms, however, while they resemble the earthworm in most respects, lead a free and predacious existence. Of these the genus *Nereis*, of which several species are found on our coasts, is a good example ; *Nereis cultrifera* (Fig. 13.19) is common under stones on the south coast of England, where it is known as the red cat and is used as bait. The body of this worm is about six inches in length, of a greenish colour, with red on the limbs and where the dorsal blood vessel shows through, roughly cylindrical, tapering towards the hinder end, and divided into about eighty segments. Like the earthworm, it is covered with a thin cuticle, but each somite has instead of a small number of short chætæ protruding directly from the body-wall, a pair of

flat, hollow vertical movable lobes called parapodia bearing many longer chætæ (Fig. 13.20). Each parapodium is cleft into two principal lobes, a dorsal notopodium and a ventral neuropodium. Each of these is again divided into smaller lobes and bears at its base a slender process known as a cirrus. A stout, deeply embedded chæta or aciculum, which does not project to the exterior, supports the notopodium and another the neuropodium, and each of these bears a tuft of other chætæ. In the sexually mature stage of the

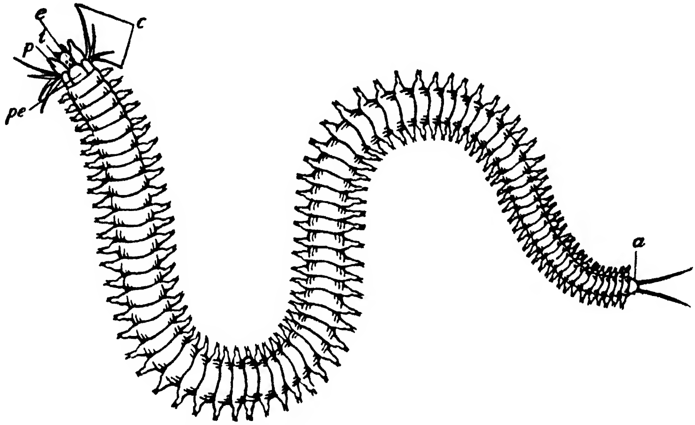


FIG. 13.19.—*Nereis cultrifera*.—From Thomson.

a., Anus ; *c.*, tentacular cirri ; *e.*, eyes; *p.*, palp ; *pe.*, peristomium ; *t.*, tentacles.

worm known as *Heteronereis* these are oar-shaped and there are additional complications in the parapodia. The front end of the body is modified to form a definite head (Fig. 13.21). This consists of the prostomium and the peristomium. On the prostomium are situated dorsally a pair of prostomial tentacles and two pairs of eyes, each of which is a pit lined by pigmented cells and enclosing a gelatinous mass which serves as a lens. Ventrally the prostomium bears a pair of stout palps. The peristomium carries on each side two pairs of long, slender tentacular cirri, and probably corresponds to two fused somites. Behind the last segment is a conical region without parapodia which bears a pair of slender anal cirri and the terminal anus.

The musculature of *Nereis* is more complicated than that of the earthworm, the longitudinal muscle fibres being grouped into four powerful longitudinal bundles, two dorsal and two ventral, while there are oblique muscles to move

the parapodia. As might be expected from the better provision of sense organs on the head, the brain also is more

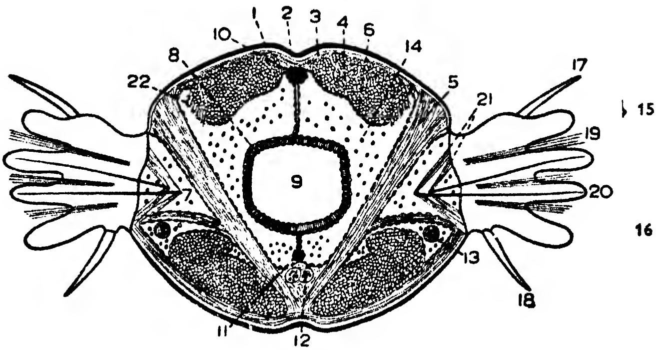


FIG. 13.20.—A transverse section through *Nereis cultrifera*, slightly simplified. The parapodia are shown in perspective. Magnified.—After Shipley and MacBride, with modifications.

1, Cuticle; 2, epidermis; 3, circular muscles; 4, longitudinal muscles; 5, oblique muscles forming a partition; 6, somatic layer of peritoneal epithelium; 7, cœlom; 8, splanchnic layer of epithelium; 9, cavity of intestine; 10, dorsal blood vessel; 11, ventral blood vessel; 12, ventral nerve cord; 13, nephridium in section; 14, ova; 15, notopodium; 16, neuropodium; 17, dorsal cirrus; 18, ventral cirrus; 19, chætæ; 20, aciculum; 21, muscles which protrude the acicula, and thus the noto- and neuropodium; 22, ciliated organ (vestige of cœlomoduct).

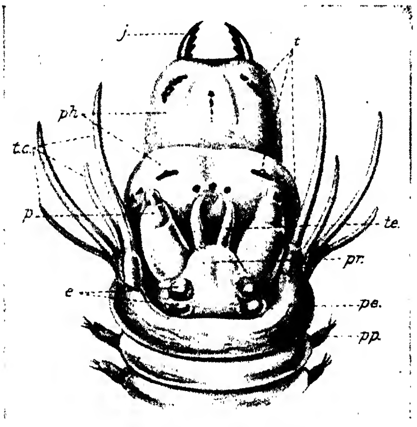


FIG. 13.21.—The head of *Nereis*, with the pharynx protruded.

e., Eyes; *j.*, jaw; *p.*, palp; *pe.*, peristomium (first two segments fused); *ph.*, pharynx; *pp.*, first ordinary parapodium; *pr.*, prostomium; *t.*, accessory teeth; *tc.*, tentacular cirri; *te.*, tentacle.

complex. The alimentary canal is simpler than that of the earthworm; the pharynx can be caused to protrude by being turned inside out, and is lined with cuticle, thickened in places to form numerous small teeth and a pair of strong jaws with

which the prey is seized. The sexes are separate. The reproductive organs are very simple, consisting of temporary masses of cells, which arise from the cœlomic epithelium. The sexually mature heteronereid forms differ from the less active asexual stage not only in the chætæ but in having larger eyes and in certain other respects. They swarm near the surface of the sea, and the ova and sperm probably escape through ruptures of the body-wall; fertilisation takes place in the water. The free young are at first very unlike the parents, being minute, globular creatures, known as trochospheres or trochophores (Fig. 13.22 *A*), which swim by means of a girdle of cilia in front of the mouth and have an apical tuft at the upper pole. They undergo a gradual change into the adult, becoming oval and then lengthening and segmenting. The larva of *Nereis* is not in all respects a typical trochosphere, having no blastocœle (p. 636). In Fig. 13.22 *B* a more typical example is shown, in a later stage of development than that represented in Fig. 13.22 *A*.

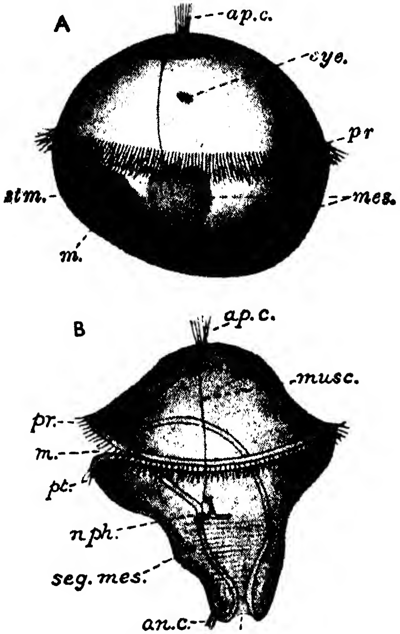


FIG. 13.22.—*A*, The trochosphere of *Nereis*.—Modified, after Wilson.

B, A typical trochosphere in an early stage of the transformation into the adult.

an., Anus; *an.c.*, anal tuft of cilia; *ap.c.*, apical tuft of cilia; *eye*; *m.*, opening of mouth; *mes.*, mesoderm; *musc.*, larval muscles; *nph.*, larval nephridium; *pr.*, preoral ring of cilia; *pt.*, postoral ring; *seg.mes.*, segments beginning to form in the mesoderm; *stm.*, stomodæum (the pouch of ectoderm which forms the mouth and gullet).

HIRUDO MEDICINALIS

THE MEDICINAL LEECH

The leeches are another group of segmented worms related to the earthworms. *Hirudo medicinalis*, the medicinal leech, a dweller in freshwater pools, marshes, and sluggish streams, was becoming rare, as readers of Wordsworth will remember, a

century and a half ago, but it is still found in the Lake District, in the New Forest, and in some other places in Great Britain. It is commoner on the Continent, where, when it was more used in medicine than at present, it was bred in large numbers in special ponds. It lives normally by sucking the blood of frogs and fishes, but when it is full grown it takes also that of warm-blooded animals, and it will feed on man, though to induce it to do so his skin may have to be moistened with blood or milk or pierced by a small cut. An active specimen will draw three or four cubic centimetres of blood. The body of the leech varies in length, according to the state of contraction ; at its maximum it is about six inches and somewhat flattened, and it is provided at each end with a downward-facing sucker. It is encircled by 95 minute rings or annuli (Fig. 13.23), and brightly marked in various shades of green, yellow, and black, paler below than above.The annuli do not indicate the true segmentation. In the greater part of the body five of these lesser rings go to a segment, but towards the ends there are fewer, and in the head or region of the anterior sucker (prostomium and first five segments) there are eleven annuli, while the posterior sucker represents seven segments fused without annulation. Unlike that of the earthworm or *Nereis*, the number of segments is a definite one, amounting in all to 32, including those of the head and hinder sucker. The mouth lies in the midst of the anterior sucker, and the anus is a minute opening above the base of the hinder sucker. The male and female genital openings are median on the second annuli of the 10th and 11th segments respectively. On the last annulus of each segment from the sixth to the twenty-second, are the openings of a pair of nephridia. On the first annulus of each segment is a transverse row of minute sense-papillæ. On the head a pair of these in each segment are transformed into minute eyes, recognisable by their pigment as dark spots. There are no chætæ. The worm can walk by looping like a ‘ looper ’ caterpillar, and swim by undulation of its body.

The body is covered by a thin cuticle (Fig. 13.24), which is shed from time to time. Under this lies an epidermis, between the bases of whose cells run blood capillaries, so that the skin is a respiratory organ, in which the blood is exposed to the surrounding water. Below are circular and longitudinal muscle-layers, and within these a layer of botryoidal tissue, composed of branched canals, whose walls are laden with black pigment, while their cavity is

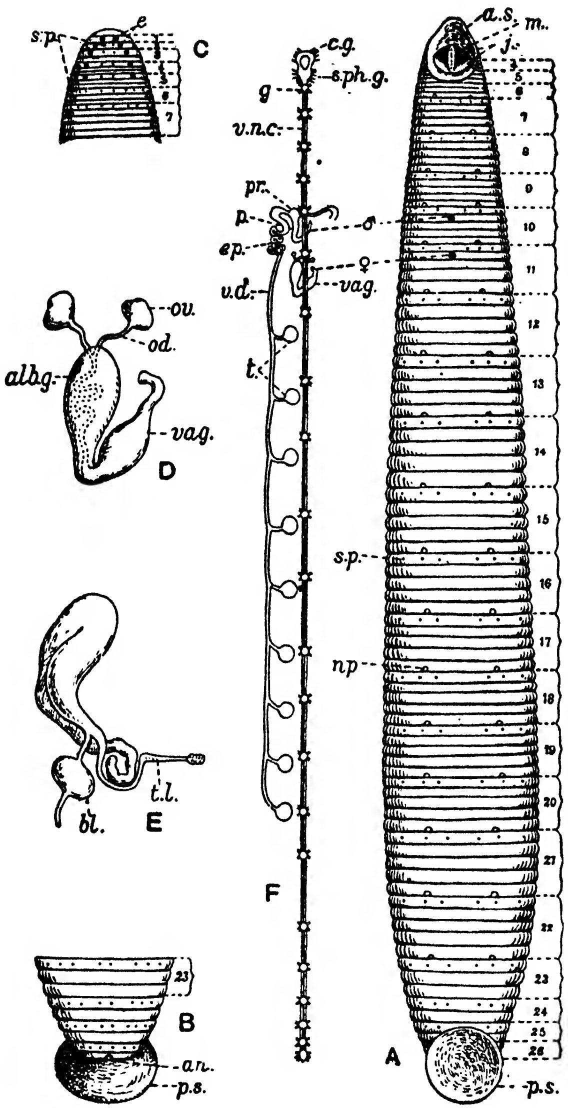


FIG. 13.23.—The medicinal leech (*Hirudo medicinalis*), and details of its anatomy.

A, Ventral view ; *B*, dorsal view of hinder end ; *C*, dorsal view of head and succeeding region ; *D*, female genital organs ; *E*, anterior view of nephridium ; *F*, nervous and genital organs (male organs of right side removed).

a.s., Anterior sucker ; *alb.g.*, albumen gland ; *an.*, anus ; *bl.*, bladder ; *c.g.*, cerebral ganglion ; *e.*, eyes ; *ep.*, epididymis ; *g.*, second ganglion of ventral cord ; *j.*, jaws ; *m.*, mouth ; *np.*, nephridiopore, by which a nephridium opens ; *od.* oviduct ; *ov.*, ovary ; *p.*, penis ; *pr.*, prostate ; *p.s.*, posterior sucker ; *s.p.*, sense papillæ ; *s.ph.g.*, subpharyngeal ganglion ; *t.*, testes ; *t.l.*, lobe of nephridium which ends in testis sinus ; *v.d.* vas deferens ; *v.n.c.*, ventral nerve cord ; *vag.*, vagina ; ♂ male opening ; ♀ female opening ; 1–26, somites.

full of blood. This tissue takes the place of a perivisceral cavity and embeds the gut. The mouth is provided with three jaws, which are compressed cushions of muscle covered with a finely toothed layer of cuticle : by these the skin of the prey is pierced with a characteristic tri-radiate wound. A muscular pharynx (Fig. 13.25) succeeds the mouth ; it sucks up the juices of the prey, and into it open numerous unicellular glands whose secretion prevents blood from clotting so that the leech's food remains

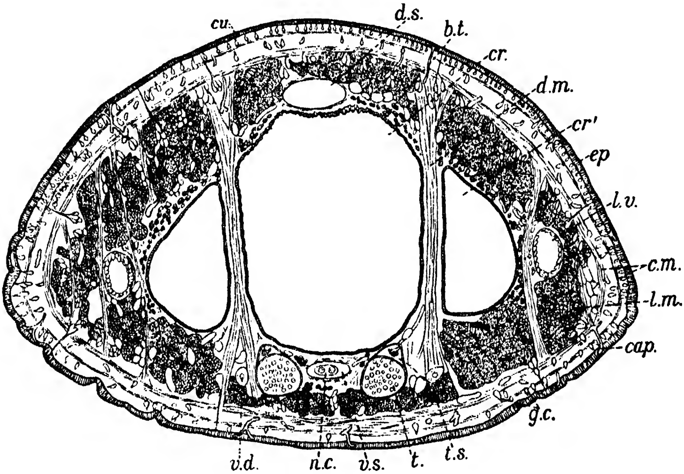


FIG. 13.24.—A transverse section of the medicinal leech.—After Bourne.

b.t., Botryoidal tissue ; *c.m.*, circular muscles ; *cap.*, capillary ; *cr.*, crop ; *cr'.*, a cæcum of the same ; *cu*; cuticle ; *d.m.*, dorsoventral muscle ; *d.s.*, dorsal sinus ; *ep.*, epidermis ; *g.c.*, gland cells ; *l.m.*, longitudinal muscles ; *l.v.*, lateral vessel ; *n.c.*, nerve cord ; *t.*, testis ; *t.s.*, testis sinus, with end of nephridium ; *v.d.*, vas deferens ; *v.s.*, ventral sinus.

fluid while it is being taken and passed backward to be digested. It is owing to this secretion that bleeding continues for some time after the leech is removed from its wound. After the pharynx comes the very large crop (segments 8–18) with eleven pairs of lateral cæca, of which the last is much larger than the rest and extends backwards on each side of the remainder of the alimentary canal. This consists of the stomach—a narrow tube, with an enlargement at its start and a spiral fold of its inner wall—the intestine, narrower than the stomach, and the rectum, somewhat wider. The blood sucked for food is stored in the crop, and passed drop by drop into the stomach, where it at once turns green and then is digested. A full meal will last the animal for several months or a year. Seventeen pairs of nephridia lie in

segments 6–22. Each is a mass of glandular tissue traversed by a system of intracellular ductules. There is no internal opening, but those which lie in the testis somites have a swollen end lying in the capsule of the testis, and bearing a number of ciliated funnels which do not communicate with the ductules. There are two systems of tubes which contain a fluid like blood—a red plasma with a few colourless corpuscles. One of these systems is the true blood-vascular system : its principal vessels are two contractile lateral trunks, which unite before and behind, and are connected also by a network of capillaries. The other vascular system consists of a dorsal and a ventral longitudinal sinus, which are also connected before and behind and by means of a capillary system. The walls of this system are thinner than those of the true blood vessels. They represent the cœlom, as may be seen from the fact that the ventral sinus encloses the nerve cord and communicates with capsules around the ovaries and testes. The botryoidal tubes are also in communication with the sinus system. It is said that the capillaries of the true blood system are connected with it. The nervous system is of the same type as those of the earthworm and *Nereis*. A small brain, above and before the pharynx, is connected by a pair of very short circumpharyngeal commissures with a ventral cord which carries at wide intervals twenty-three ganglia. Of these the first or subpharyngeal and the last each represent several fused. Nerves are given off from the brain and the ganglia. The commissures which unite the ganglia of the ventral cord are seen in section to be double, with a slender median strand.

FIG 13.25.—A diagrammatic view of the alimentary canal of the medicinal leech, as seen when it is not gorged with blood.

*cr.*I., *cr.*II., Cæca of the crop; *int.*, intestine; *ph.*, pharynx; *rm.*, rectum; *st.*, stomach.

The animal is hermaphrodite. There are nine pairs of testes, enclosed in spherical capsules in the 12th–20th somites, with on each side a common vas deferens, which is coiled as an ‘ epididymis ’ in the 10th somite, where the vasa deferentia join to open on a muscular, protrusible penis, surrounded at its base by a ‘ prostate ’ gland. The single pair of ovaries lies in the 11th

somite, in which its short oviducts open by a common vagina. The eggs are laid in cocoons secreted by 'clitellar' glands in the skin of the 10th–12th segments and placed in holes made in the banks, above water. The young resemble the parents and feed at first on the juices of water insects and the like.

ANNELIDA

The phylum Annelida, to which the creatures described in this chapter belong, is very difficult to define, since its most distinctive features are not possessed by all its members. Annelids are segmented animals with one preoral segment, the prostomium, but all their other universal characteristics they share with other groups; they are triploblastic and cœlomate; the nervous system consists of a double ventral cord, usually with a pair of ganglia in each segment, and of a pair of commissures surrounding the gut and leading to a pair of preoral ganglia; they have nephridia and cœlomoducts; the larva if present is a trochosphere. Negative characters of importance are the absence of any well-formed appendages except in connection with the mouth (the parapodia do not qualify as such) and the absence of a continuous thick chitinous exoskeleton. Typical members of the phylum possess chætæ. Some of the above characters are discussed more fully in the next chapter.

CLASS I—CHÆTOPODA

Chætæ are present and the cœlom is well developed. There are two Orders.

ORDER I—POLYCHÆTA

The chætæ on each somite are many and parapodia are characteristic; the head is comparatively well developed, with cirri, tentacles, and jaw apparatus; gills are frequent; the sexes are usually separate, fertilisation is external, and the larva is a trochosphere.

The polychætes are marine, and are divided ecologically into the errant forms, which are typically free swimming, though they sometimes live in temporary burrows, and the sedentary forms, which are subdivided into those which are tubicolous, that is, live in formed tubes which they seldom or never leave, and those

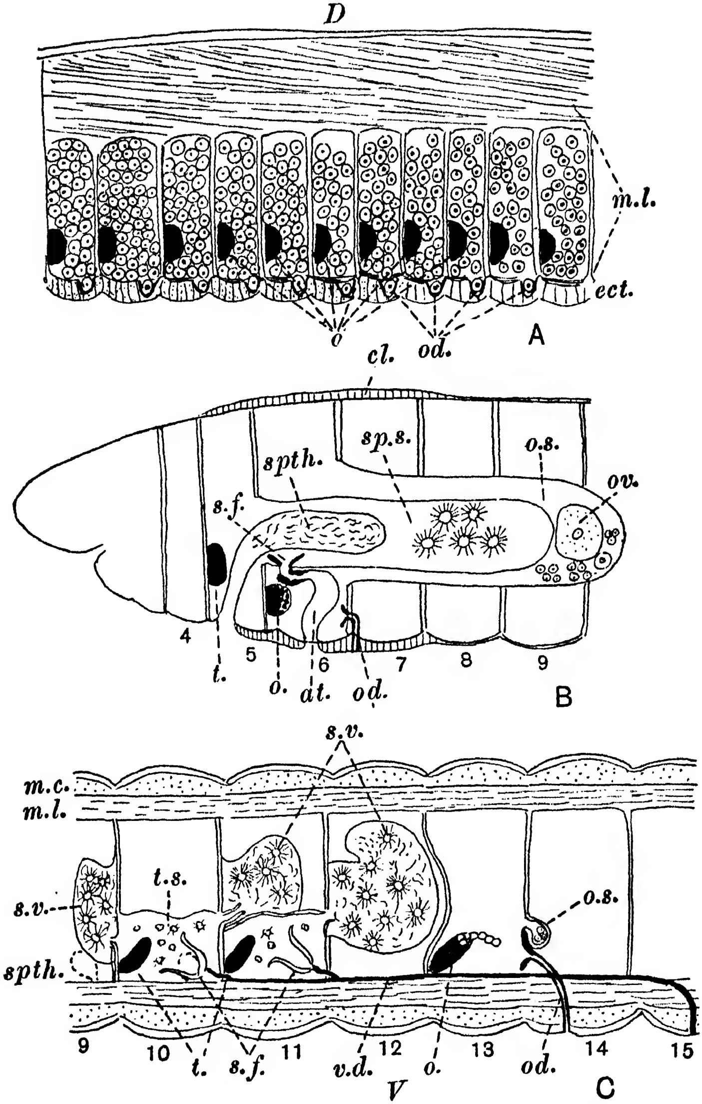


FIG. 13.26.—Reproductive organs of the chætopoda in diagrammatic longitudinal section.—From Borradaile and Potts, *The Invertebrata*, 2nd edition, 1935. Cambridge University Press.

A, *Serpula intestinalis* (Polychæta); *B*, Naididæ (Oligochæta); *C*, *L. terrestris*.—*D*, after Stephenson; *C*, after Hesse. *D*, dorsal and *V*, ventral. The numbers are those of the segments, the vertical lines are septa.

at., Atrium; *cl.*, clitellum; *ect.*, ectoderm; *m.c.*, circular muscles; *m.l.*, longitudinal muscles; *o.*, ovary; *od.*, oviduct; *os.*, ovisac; *ov.*, ovum; *s.f.*, funnels of vas deferens; *sp.s.*, sperm sac; *s.v.*, seminal vesicle; *spth.*, spermatheca; *t.*, testis; *t.s.*, testis sac; *v.d.*, vas deferens.

which burrow in soft sand. The body, especially the head region, is generally modified to suit the mode of life. *Nereis* is a typical errant genus, *Serpula* lives in little tubes of calcium carbonate attached to rocks, and *Arenicola*, the lug worm, is a burrowing form living between tide-marks.

ORDER II—OLIGOCHÆTA

The characters are in general the reverse of those of the polychætes. A clitellum is present. They are terrestrial or freshwater in habitat, *Lumbricus* being an example of the first, and *Nais*, common in ponds, of the second.

CLASS II—HIRUDINEA

These are the leeches. They have 32 segments and two ventral suckers. Chætæ are absent except in some primitive forms; the cœlom is reduced; they are hermaphrodite, with a clitellum and a rudimentary cocoon and direct development. *Hirudo* is an example, and another is *Aulostomum* (=*Hæmopis*), the smaller horse-leech, which is common in ponds. In the tropics there are terrestrial species.

Other classes of annelids of lesser importance are the Archiannelida and the Gephyrea.

14

THE CŒLOMATE BODY

WITH the annelids we meet the type of body structure which is found in all the remaining groups of the animal kingdom. It seems to have been adequate for all the developments required for different types of habit and habitat, and although there are many modifications and some regressions there are no changes in the basic plan. In this chapter the chief characters of the cœlomate body, as it is called, are briefly described ; for details the chapters dealing with the various types should be consulted. The basic plan is an arrangement of three layers of tissue, with, in the middle one, a series of spaces. Generally speaking the inner and outer layers are formed in the embryo simultaneously, and before the middle one ; the inner one is called the hypoblast, and the tissues to which it gives rise are known collectively as endoderm. This forms the lining of most of the gut and little else. The outer layer is similarly called the epiblast, and the tissues which it forms are the ectoderm. This is chiefly the outer parts of the skin (and outgrowths from this such as hair and feathers) but it includes also the nervous system. Between the hypoblast and the epiblast, and generally formed a little later, often from the hypoblast, is the mesoblast. It gives rise to the mesoderm, which includes almost all the other tissues of the body : muscles, gonads, often the excretory organs, and in the vertebrates the skeleton. The three germ layers, as hypoblast, mesoblast, and epiblast are called, are not layers of cells in the sense in which one speaks of layers of chocolates in a box, but in the sense in which the term is applied to a sandwich, to describe plates of material, of different origin, separated from their neighbours ; that is to say, any of the germ layers may be more than one cell thick. In addition to the annelids and those groups which we have not yet described, the flatworms and roundworms have three germ layers ; all these animals are known collectively as Triploblastica, in distinction from the cœlenterates, which have no mesoderm and are Diploblastica. The gonads of the cœlenterates are in the ectoderm or endoderm according to the class, but they have little other specialisation of tissue. The mesoglœa is non-cellular, and corresponds to the mesoblast in little else besides position.

BILATERAL SYMMETRY

All triploblastic animals early acquire bilateral symmetry, so that there is a median plane on either side of which are two halves of the body which are roughly mirror images of each other. In the annelids there is little difference between the two sides, but in the molluscs and chordates there is a greater or lesser degree of secondary internal asymmetry, especially noticeable in the coiling of the gut, but often showing itself in blood vessels, gonads or other organs. The external appearance of similar right and left sides is usually maintained much more closely, although differences are sometimes apparent, as in the pincers of the crayfish and the scrotum of many mammals. The echinoderms completely lose their bilateral symmetry early in embryonic life, and acquire a secondary radial symmetry.

The existence of bilateral symmetry enables us to distinguish between anterior and posterior ends, between right and left sides, and between dorsal and ventral surfaces. A section cut parallel to the anteroposterior axis and in a vertical plane is called longitudinal, and if it is in the middle line it is sagittal. A horizontal section is called frontal, and one which is at right angles to the axis is transverse. The surface of a structure nearer to the axis of symmetry is called medial, that further away is lateral, but these terms are not often used outside human anatomy. The end of a structure such as a limb which is nearer to the body is called proximal, that further away is distal.

THE CŒLOM

The flatworms and roundworms are solid, except for the gut and excretory and genital canals. All the other triploblastic groups have two large series of spaces in the mesoderm, although sometimes these are reduced. The most obvious of these is the cœlom, often called simply the body cavity. It is sometimes formed from pouches which grow out from the gut while the mesoblast is being formed, sometimes by a separation of mesoderm cells to form a space. Its simplest shape is that of a trough-like cavity (in vertical transverse section like a U) partly surrounding the gut, but it is often divided up in various ways. The cœlom contains a fluid, in which there may be cells, but it is doubtful if the cavity itself can truthfully be said to have any

function. The fluid no doubt acts as a shock-absorber for the viscera, which hang in it, and the cells may be excretory, as they are in the earthworm. Its walls generally give rise to the ova and spermatozoa, and may help in excretion, as they do in the vertebrate kidney (p. 626). The cœlom always has openings to the exterior. In Annelida there are dorsal pores, and in the dogfish abdominal pores; these seem to be holes of no well-defined homology or purpose, and perhaps act merely as safety-valves, allowing cœlomic fluid to escape if the pressure becomes too great. More important are cœlomoducts, which are paired tubes, often segmental, which grow out laterally from the walls of the cœlom so that they are made entirely of mesoderm. They are the route by which the gametes escape, and may become highly specialised genital ducts, and in the vertebrates they form the excretory tubes. In many annelids, such as the earthworm, the nephridia, which are ingrowths from the ectoderm, may pierce the wall of the cœlom and form a third type of communication with the exterior. In many polychætes each nephridium becomes intimately attached to a cœlomoduct to form a composite structure called a nephromixium.

THE HÆMOCŒLE

The other space in the mesoderm is the hæmocœle, or the cavity of the blood-vascular system. This is sometimes, as in the earthworm, directly derived from the spaces between the cells of the early embryo; in such animals it is a part of the external environment which has come to be surrounded by cells, and into which fluid is secreted and cells wander. Sometimes, however, as in the vertebrates, it is formed by the separation of mesoderm cells along definite lines, some of the cells being left as the blood corpuscles. Whatever its origin it is always developed as a branching system of vessels with definite walls, which in places are muscular and contractile. In the arthropods and molluscs the blood-vascular system is also expanded in places to surround the other organs much as the cœlom does in a vertebrate, and is called open, in distinction from a closed system with capillaries; such creatures have the cœlom reduced, and although formally cœlomate are very different from other such animals. The term hæmocœle is sometimes restricted to these organ-containing expansions of the cavity of the blood system. The hæmocœle is sometimes called the primary body cavity, on account of its derivation from the

chinks between the cells of the embryo, and the cœlom the secondary body cavity. Since in many embryos this temporal distinction cannot be made, and since neither is ever present in an adult animal without the other and they add nothing in meaning, these terms are best abandoned.

FUNCTIONS OF BLOOD

The properties of the blood, the fluid and cells present in the blood-vascular system, are usually listed as many, but all the important ones can be summed up in one word : transport. The mesoderm enables an animal to become large ; bulk prevents easy access to the cells by simple diffusion across adjacent cells, and so a transport system becomes necessary. The things which are carried to the cells are oxygen, either in solution or in chemical combination with a substance such as hæmoglobin ; food, chiefly as amino acids and hexoses, and hormones (p. 16). These last are known in vertebrates, cephalopods, insects, crustaceans and annelids, that is, in all the chief phyla with blood. From the cells the blood takes excretory products, including carbon dioxide, and heat. In large animals the latter is very important, for a cell in the middle of a big mass of muscle is well insulated, and if there were no cooling system it would overheat. The fact that in insects, where oxygen is carried by different means, the blood system is far less well developed than it is in other arthropods, suggests that oxygen-transport is the most important function of the blood. Besides carrying substances from one place to another, the blood is also important in forming a relatively stable internal environment for the active body cells. This environment is an aqueous solution in which the main constituents are kept at an approximately constant composition ; the hydrogen ion concentration of vertebrate blood does not greatly fluctuate, even though large quantities of lactic acid and carbon dioxide are put into it, because it is well buffered with phosphate. Other ions, and substances such as glucose, are kept constant by the co-operation of the kidney, which eliminates them if they are present in excess and holds them back if there is not enough of them. Other excretory organs, such as the nephridia of the earthworm and the green glands of the crayfish, act in a similar, but probably less elaborate, way.

These are the fundamental functions of blood, which would

have to be carried out somehow even if the animal had no blood system ; it is difficult to imagine that any of them, with the partial exception of oxygen transport, which in small animals may be done by a system of air-containing tubes, could be properly carried out except by a circulating liquid. Various types of animal have also taken advantage of the existence of blood to use it for other and minor purposes, which can equally well be fulfilled in other ways. It is an accident that the oxygen-carrying substances contained in most bloods are pigments, and in a number of animals they are visible from the outside, possibly or probably to the advantage of the species. The most familiar example is man himself, for in the white races the colour of the hæmoglobin is presumably important in sexual selection, but its most striking use is seen in some monkeys, where the chest or buttocks blush vividly in excitement. As is well known, a fluid can transmit a pressure and so be used to increase a volume, and these properties have more than once been used by animals. The swan mussel moves by pushing its foot forward through the mud and then inflating it with blood. When the muscles which withdraw the foot are contracted, the latter is stuck fast, and so the whole animal is pulled forward ; the blood is then withdrawn and the process repeated. The swelling of the labium of blood-sucking insects, the eversion of the insect-catching tongue of the chamæleon, and the increase in size and stiffness of the mammalian penis necessary for copulation, are brought about in a similar way. The method used in all these instances is largely the same ; the veins are constricted so that the blood which is pumped in by the heart can only escape slowly and is retained under pressure. The resulting turgidity is comparable to that which is normal in herbaceous plants, although here the fluid is enclosed and its pressure is osmotic, not hydrostatic, in origin. In both the Amphibia and the insects the phagocytes in the blood assist in metamorphosis by ingesting unwanted material, such as the tadpole's tail, and transferring it elsewhere. Finally, in mammals and birds, the blood-vascular system, rather than the blood itself, is used in temperature regulation. Although the blood takes no direct part in temperature control, its presence and circulation are necessary to the efficient working of such control, just as a stirrer increases the efficiency of a thermostat. In large animals without temperature regulation the blood is probably important in preventing local rises of

temperature in active organs by conveying heat away to the surface or to less active regions of the body. This was probably very important in the large extinct reptiles (unless, as some people think, these creatures must have had a proper regulating mechanism).

Although blood seems to be necessary for a large animal, its possession brings dangers. A fluid under pressure is easily lost if the vessel which contains it is pierced, and a medium which takes food and oxygen to the body cells is an ideal environment for parasites, so that it is not surprising that devices have been developed to overcome these dangers ; they are not functions of blood, since if blood did not exist they would be unnecessary, but they are important properties of it. It is not the function of a motor car to have brakes, but they are necessary in order that it can safely perform its function of transporting people from place to place. Excessive loss of blood by bleeding is prevented because on exposure to air blood forms a clot ; parasites are attacked by phagocytes, and the poisons which they produce are inactivated by antitoxins (p. 149).

Many of the functions of blood may be carried out, often in a less efficient way, by the cœlomic fluid. It must maintain something of a constant environment ; it carries excretory products and contains phagocytes ; and in the earthworm it transmits the pressures produced by the muscles so that burrowing is possible.

SEGMENTATION

A division into parts, or segments in a loose and general sense, is common in animals. The egg is sometimes said to segment when it divides into cells or blastomeres ; the limbs of arthropods are divided into jointed parts or podomeres ; and the tapeworm grows a linear succession of proglottides, the oldest being farthest from the growing point. In many cœlomates there is a different type of repetition of parts, in which the growing point remains posterior. This is known as metameric segmentation, or often simply as segmentation ; and the repeated parts are called segments or metameres. It seems to be dependent on the mesoderm, for the endoderm and ectoderm are never fully divided, although they may secondarily have to follow the pattern imposed on them by the mesoderm, the segmentally arranged embryonic blocks of which are called somites. In an extreme case muscles.

glands, gonads, cœlomoducts, nephridia, ganglia, and nerves may be repeated in almost indistinguishable units down the body. Such a state is found in many polychætes. The earthworm has fairly complete segmentation, but the gonads are confined to one or two segments and the distribution of the accessory sexual organs such as seminal vesicles makes many of the anterior segments distinct. The segmentation of the crayfish and of insects is more superficial, and there is little visible internally, but the continuous exoskeleton makes external jointing functionally important. The embryos of vertebrates have a conspicuous and fundamental segmentation ; in the fishes much of this persists in the adult, but in the other classes practically no traces of it are left. Even the vertebræ, which appear to be obviously segmental, do not correspond to the segments of the embryo.

Many segmented animals have the first few segments much modified to form a head. This process is known as cephalisation ; it occurs to some extent in *Nereis*, and is conspicuous in the insects and vertebrates. The changes generally include the development of special limbs or other structures around or in the mouth ; the specialisation of sense cells and their association with other types of cell to form conspicuous organs such as eyes ; and internally the concentration of nervous tissue into a brain. Cephalisation is generally regarded as an inevitable result of always moving forwards, and it certainly seems reasonable that that part of the body which first meets food and first learns about the outside world should be specialised to eat and see. It is only, however, in segmented animals that cephalisation is highly developed ; the most highly organised unsegmented animals, the molluscs, do indeed have something of a head, but it is remarkable that in many cephalopods, where it is best developed, it is pretty well in the middle of the body, and that these creatures move backwards much more rapidly than forwards. The octopus, alone amongst animals, bears any resemblance to Shakespeare's ' Men whose heads, Do grow beneath their shoulders '.

OSMOTIC REGULATION

It is a general property of living membranes that they are semipermeable, that is, allow some substances, especially water, to pass through them much more rapidly than do others. A result of this property is that when they separate two aqueous solutions

of different strengths, water passes across them from the weaker to the stronger solution (a phenomenon known as osmosis), with consequent swelling and increase of pressure. For most animals living in the sea the semipermeability of living matter is of little consequence, for their protoplasm has much the same concentration of solutes as has sea water, so that there is little movement of water. In fresh water things are different, and the prevention of osmosis is important for animals living there ; it is especially so in animals with a body cavity, for here not only do the cell walls act as semipermeable membranes, but so do the tissues themselves, causing water to be attracted into the cœlomic fluid or blood. The most awkward situation of all is that of estuaries, where there is a large daily change in the external salt concentration. According to their osmotic relations animals may be classified into two or three groups. First are most of those which live in the sea, including the majority of invertebrates and the cartilaginous fishes ; their environment does not normally change, and they have no means of coping with any osmotic changes that do occur ; they are called stenohaline. If put into fresh water they absorb it. Secondly, some invertebrates, such as the shore crab and *Nereis diversicolor*, live where sea water and fresh water mix, so that the salt concentration is continually changing, and many bony fishes, such as the salmon, pass from the sea into rivers and back again. They are able, to a greater or lesser extent, to prevent the entry of water, or to expel it after it has entered, and are called euryhaline, as the salt concentration in their body fluids remains approximately constant. Although living in a constant environment the marine bony fish also have to regulate and are euryhaline ; their blood has a lower salt concentration than sea water, so that water tends to leave them. The animals which live permanently in fresh water are also able to regulate their salt concentration in the sense that they can cope with a tendency of water to enter, but they may for various reasons be unable to survive in sea water, so that while osmotically they are euryhaline ecologically they make a third class. Osmotic regulation may be carried out by a special organ, such as the contractile vacuole of Protozoa, but more often use is made of an organ which has other functions as well. The shore crab and fish use their gills, and most euryhaline cœlomates their excretory organ. In vertebrates the relative impermeability of the skin is important.

15

THE CRAYFISH

CRAYFISHES are found in many English rivers, especially in those which rise in chalk or limestone hills. They are little, lobster-like creatures, which make burrows in the river banks. They dislike strong light and during the daytime generally remain in their holes with only their pincers and long feelers projecting. When they come out they crawl stealthily about, searching constantly for their food, which consists of organic matter of any kind, plant or animal, dead or alive, that they are able to seize and break up with their pincers. If danger threatens, they dart backward suddenly and swiftly. They are used for food, especially for garnishing salads, and were formerly caught in large numbers in this country by means of wicker crayfish-pots, but in 1887 their numbers were greatly reduced by a disease. The name is also used for a number of related genera in various parts of the world.

EXTERNAL FEATURES

The English crayfish, *Astacus pallipes* (Fig. 15.1), is about three inches long, and of a dull, greenish colour, which harmonises well with the surroundings in which it lives. A number of other species are found on the Continent. The body of a crayfish is armoured with a thick cuticle. It is segmented, each segment bearing a pair of jointed limbs, but in the front part the segments are fused to form a fore-body or cephalothorax, where the only conspicuous sign of their existence is the presence of several pairs of limbs, though parts of the armour and certain internal organs are also segmentally arranged. The rest of the body, known as the hind body or abdomen, is more completely segmented. At the end of the abdomen is a flat piece known as the telson, on the under side of which the anus opens. The telson bears no limbs, and is divided by an imperfect transverse joint. The armour of each segment of the abdomen consists of a broad back-piece or tergum and a narrow belly-plate or sternum, with a pair of V-shaped prolongations, known as the pleura, joining them at the sides. There are no pleura on the first abdominal

somite. The tergum, sternum, and pleura of each somite form a continuous ring. The limbs are jointed to the hinder side of the sternum near its outer ends, and the part of the sternum between each limb and the adjoining pleuron is sometimes called an epimeron. The terga overlap one another from before backwards and slide over one another as the abdomen is straightened and bent, the armour of each somite being joined to that of the next by thin cuticle, which allows of movement. In the cephalothorax the terga are fused to form a shield or carapace. This is prolonged in front into a beak-like rostrum and is crossed by a furrow, which is called the cervical groove because it is supposed to mark the separation of the head and thorax. At each side of the body a fold of the carapace overhangs as a lean-to roof, the gill cover or branchiostegite, which encloses between itself and the side of the body a chamber in which the gills lie. Behind the cervical groove a branchiocardiac groove on each side marks off the branchiostegite from a median cardiac region which roofs the thorax. The cuticle of the inside of the branchiostegite and part of the side of the body underneath it are thin. On the ventral side of the cephalothorax the limbs of each pair are close together, but small sterna lie between them. The mouth is placed on the ventral surface at some distance from the front end, and in front of it the sternal surface slopes upwards to the rostrum. At the sides of the latter, upon a pair of short, movable stalks, are placed the eyes, and below these stand two pairs of feelers or antennæ.

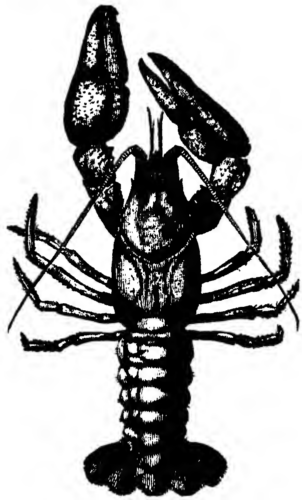


FIG. 15.1.—View of a crayfish from above.—After Huxley. Note cervical groove, cardiac region of carapace, rostrum, and tail fan.

LIMBS

The limbs or appendages number nineteen pairs, without counting the eyes, which are by some authorities reckoned as limbs. We shall not take this view, but as there is evidence in the development of the crayfish and of related animals that the

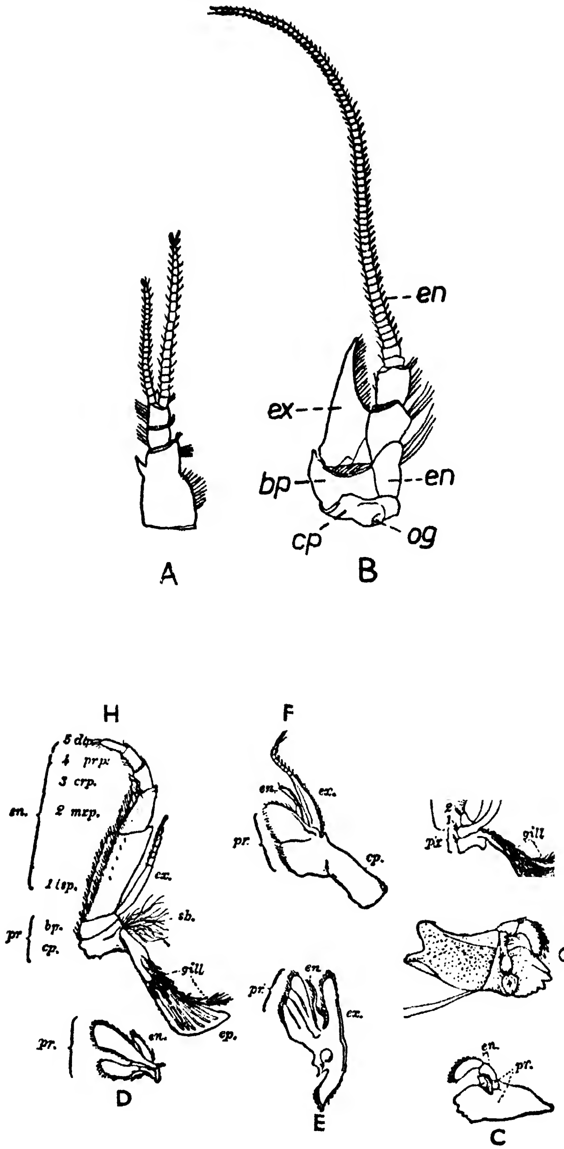


FIG. 15.2.—The anterior appendages of the left side of a crayfish.

A, External view of the antennule of the left side; *B*, ventral view of the antenna of the right side; *C*, mandible in ventral view; *C′*, the same in dorsal view, somewhat enlarged, showing molar process; *D*, maxillule (first maxilla); *E*, maxilla (second maxilla); *F*, first maxilliped; *G*, second maxilliped; *H*, third maxilliped.

bp., Basipodite; *cp.*, coxopodite; *crp.*, carpopodite; *dtp.*, dactylopodite; *en.*, endopodite; *ep.*, epipodite; *ex.*, exopodite; *gill*; *isp.*, ischiopodite; *mrp.*, meropodite; *o.g.*, opening of the green gland; *pr.*, protopodite; *prp.*, propodite; *sb.*, setobranch or tuft of coxopodite setæ; 1–5, joints of endopodite.

foremost region of the head corresponds to a somite, we shall regard the body as containing twenty segments, of which the foremost bears no limbs. The telson is not a segment. Of the twenty segments, the first six form the head, the next eight the thorax, and the last six, with the telson, the abdomen. The parts of which a complete limb consists are best seen in the limbs known as the third pair of maxillipeds (Fig. 15.2 H), which lie immediately in front of the great pincers. This illustrates fairly well the type of crustacean appendage called the biramous limb or stenopodium, which has a base or protopodite, two branches called endopodite and exopodite, and sometimes extra processes or epipodites. The

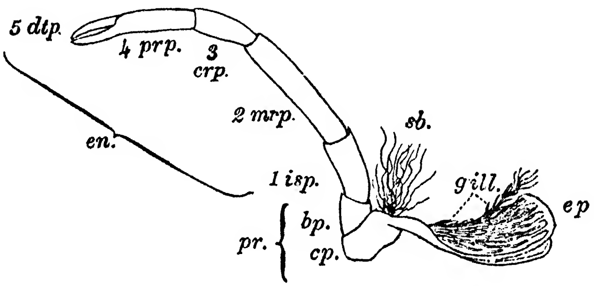


FIG. 15.2 H.—Third maxilliped; the first walking leg of a crayfish.

other limbs are built upon the same general plan as the third maxilliped, but they have modifications suited to their functions, and parts are often missing. They are shown in Fig. 15.2 F and G and Table I. More primitive crustacea have a flattened type of limb called the phyllopodium.

CUTICLE AND EPIDERMIS

The ectoderm or epidermis of the crayfish consists of a layer of protoplasm with nuclei, which in many parts is not divided into cells and is therefore a syncytium (p. 33), though in places it forms a columnar epithelium. Outside it lies a cuticle which it secretes, which contains chitin (p. 157), and is for the most part thick and hardened with salts of lime, but remains thin and flexible in certain places so as to form joints which allow the parts of the body to move upon one another, and also in the gill chambers. In places it bears bristles (setæ) of various shapes.

TABLE I

The Limbs of the Crayfish

Segment		Name	Function	Structure
Head	1	No appendage		
	2	Antennule (1st antenna)	Sensory	Three basal segments. Two branches, probably not homologous with endopodite and exopodite. Bears statocyst.
	3	Antenna (2nd antenna)	Sensory	Long endopodite. Bears opening of green gland.
	4	Mandible	Feeding	Toothed biting base and short 2-segmented endopodite making the palp.
	5	Maxillule (1st maxilla)	Feeding	Three flat plates.
	6	Maxilla (2nd maxilla)	Respiratory	Several lobes. The exopodite forms the scaphognathite or baler, which maintains a current of water over the gills.
Thorax	7	1st maxilliped	Respiratory and feeding	Large exopodite and epipodite.
	8	2nd maxilliped	Respiratory and feeding	Similar to 1st maxilliped.
	9	3rd maxilliped	Respiratory and feeding	Typical structure.
	10	Pincers (forceps, cheliped)	Fighting, holding	No exopodite. Very large endopodite with grasping chelate end.
	11	1st walking leg	Walking	As last, but much smaller.
	12	2nd walking leg	Walking and sexual	As last. Bears genital opening in female.
	13	3rd walking leg	Walking	As last, but not chelate. No genital opening.
	14	4th walking leg	Walking and sexual	As last, but no epipodite. Bears sexual opening in male.
Abdomen	15	Swimmerets	Sexual	Form canal for seminal fluid in male; vestigial in female.
	16	Swimmerets	Swimming and sexual	Modified in male; flattened endopodite and exopodite in female.
	17, 18, 19	Swimmerets	Swimming and sexual	Flattened endopodite and exopodite; carry eggs in female.
	20	Paddles	Swimming	Large flattened endopodite and exopodite form, with telson, the tail fan.

These are quite different from the chætæ of the earthworm; they are hollow, and the epidermis is continued into them and is here often connected with nerve fibres, so that the bristles

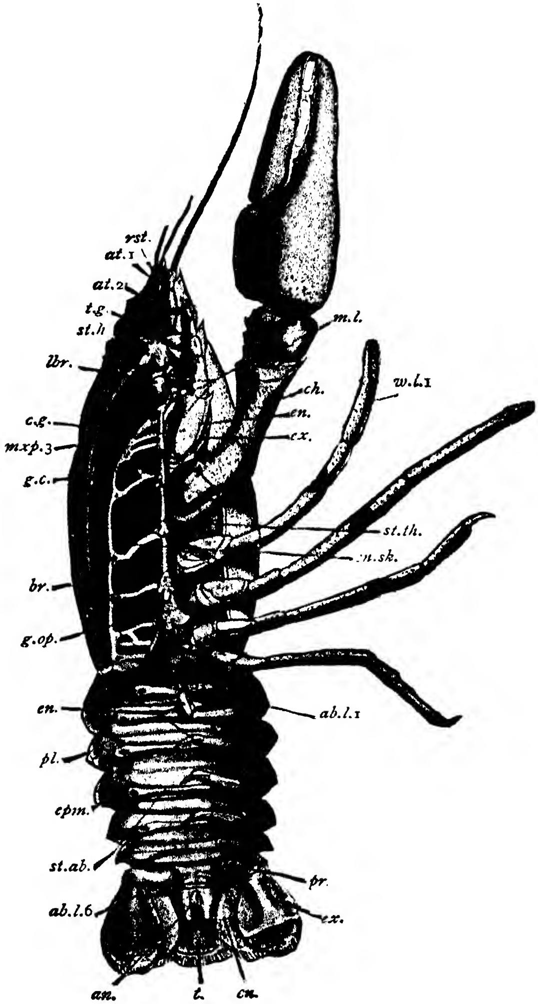


FIG. 15.3.—A ventral view of a female crayfish, with the limbs of the right side removed and the branchiostegite of that side partly cut away.—Partly after Howes.

*ab.l.*1,6, First and sixth abdominal limbs; *at.*1, antennule; *at.*2, antenna; *an.*, anus; *br.*, branchiostegite; *c.g.*, cervical groove; *ch.*, cheliped; *en.*, endopodite; *en.sk.*, endophragmal skeleton; *epm.*, epimeron; *ex.* exopodite; *g.c.*, gill chamber; *g.op.*, openings of oviduct; *lbr.*, labrum; *m.l.*, limbs adjoining the mouth; *mxp.*3, third maxilliped; *pl.*, pleuron; *pr.*, protopodite; *rst.*, rostrum; *st.ab.*, abdominal sterna; *st.h.*, sternal region of body in part of mouth; *st.th.*, thoracic sterna; *t.*, telson; *t.g.*, tubercle on which green gland opens; *w.l.*1, first walking leg.

serve as sense organs of various kinds. From time to time the cuticle is shed, a process called ecdysis, and replaced by a new one secreted beneath it; this allows of growth. Moulting takes place frequently while the animal is young, but the old male sheds its cuticle only twice a year, and the female only once. As the time for moulting draws near, a new cuticle begins to form under the old one, which is loosened from the epidermis, and the crayfish goes into hiding for some days while the new cuticle is soft, and the animal is helpless while it is hardening. The shell then splits across the back and along the limbs, and the crayfish, lying on its side, draws itself out of the old cuticle.

SKELETON, MUSCLES, AND LOCOMOTION

There is in the crayfish no continuous muscular body-wall, but numerous muscles, composed of striped fibres, move the various parts of its body, being attached to the inside of the pieces of the armour. Thus the skeleton is external, not, like that of a vertebrate, internal. Its pieces, known as sclerites, usually abut upon one another across the soft jointing membranes by hard knobs which serve as hinges. In the thorax ingrowths of the cuticle provide a kind of false internal skeleton. This has the form of a complicated scaffolding along the ventral side of the animal and is known as the endophragmal skeleton. In the limbs, as in those of vertebrates, opposing muscles (flexors and extensors) bend and straighten each joint. Ingrowths of the cuticle serve as tendons for them. The abdomen also is moved by two sets of muscles (Figs. 15.5, 15.7). A dorsal set of extensors starts from the inside of the carapace and is inserted into the terga of the abdominal somites. When they contract, these muscles draw forward the terga and thus straighten the abdomen. Ventrally, powerful and complicated flexors connect the sterna with one another and with the endophragmal skeleton (Fig. 15.7). The flexors, when they contract, draw closer the sterna and thus bend the abdomen. By this movement, spreading at the same time its tail fan, the crayfish can suddenly jump backwards to escape from its enemies. Its gentle forward movements are carried out by the walking legs, aided by a paddling of the abdominal limbs. The legs of the first three pairs pull and those of the last pair push, and their movements are carried out in such a way that the animal is always standing upon

six legs while two—which are on opposite sides and of different pairs—are in motion.

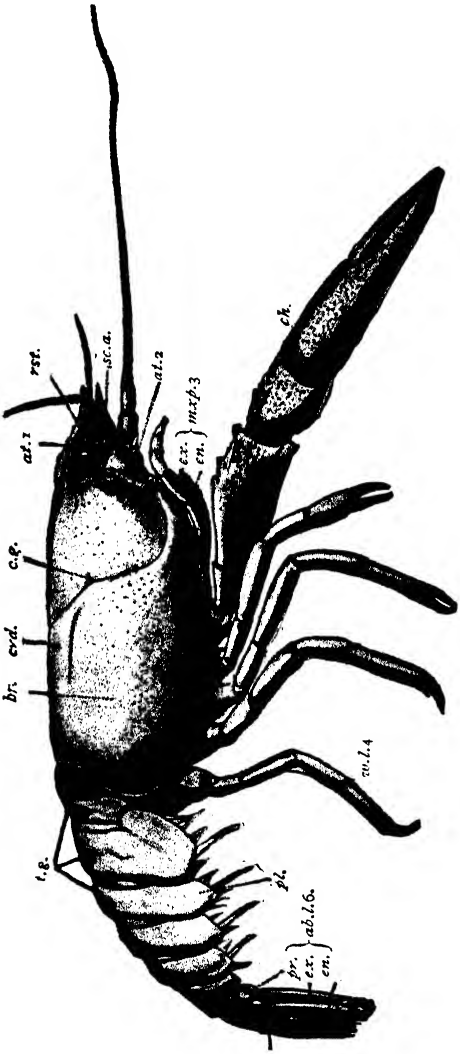


FIG. 15.4.—View of a crayfish from the right side.

ab.l.6, Sixth abdominal limb ; *at.1*, antennule ; *at.2*, antenna ; *br.*, branchiostegite ; *c.g.*, cervical groove; *ch.*, cheliped ; *crd.*, cardiac region of carapace ; *en.*, endopodite ; *ex.*, exopodite ; *mxp.3*, third maxilliped; *pl.*, pleuron ; *pr.*, protopodite ; *rt.*, rostrum ; *sc.a.*, scale of antenna ; *t.*, telson ; *tg.*, terga ; *w.l.4* last walking leg.

REGENERATION AND AUTOTOMY

The power of regeneration, though it is less in the crayfish than in earthworms and much less than in *Hydra*, is still considerable. A whole limb which is injured can be grown again. The injured leg is first cast off by a spasmodic contraction of some of its muscles which causes it to break through at the basipodite, the internal cavity—which, as we shall see, is a blood space—being here crossed by a partition which leaves only a small opening, through which the nerves and blood vessels pass. When the limb is cast off this opening is quickly closed by a blood clot, after which the cuticle grows across the wound. Beneath the scar the new limb is formed as a bud and gradually takes shape. At the next moult it becomes free, though it is still small, and it increases in size at each moult, until a normal limb has been provided. This power of casting off limbs is known as autotomy. It is sometimes used as a means of escape from enemies which have seized one of the limbs, but this is not so common in the crayfish as in some animals that are related to it.

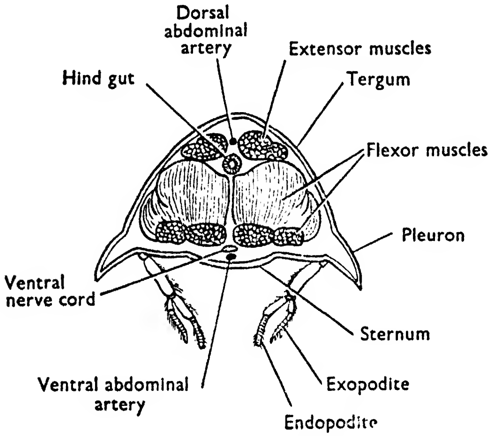


FIG. 15.5.—A semi-diagrammatic drawing of a transverse section of the abdomen of a crayfish.

PERIVISCERAL CAVITY AND ALIMENTARY SYSTEM

The body of the crayfish contains a spacious perivisceral cavity, in which the internal organs lie. This is not a cœlom, but an enlarged portion of the hæmocœle (p. 188), and communicates with the blood vessels. The alimentary canal fills the greater part of this cavity. The mouth is an elongated opening below the head between the mandibles. It has in front a wide upper lip or labrum,

and behind it is a pair of lobes (paragnatha) known together as the lower lip or metastome. A short, wide gullet leads upwards into the large proventriculus, often called the stomach (Fig. 15.6).

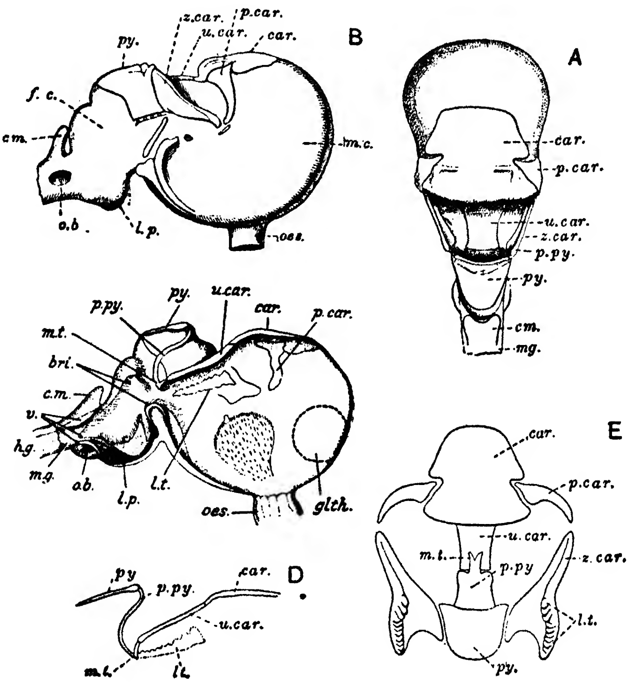


FIG. 15.6.—The proventriculus of the crayfish.

A, The whole organ from above ; *B*, the same from the right side ; *C*, the left half from within, the muscles being relaxed ; *D*, the ossicles of the mill in median section, the anterior and posterior gastric muscles being contracted ; *E*, the mill in plan. All the figures are semi-diagrammatic, much detail being omitted.

bri., Bristles for filtering ; *car.*, cardiac ossicle ; *cm.*, cæcum ; *f.c.*, pyloric or filter-chamber ; *glth.*, position of gastrolith ; *h.g.*, hind-gut ; *l.p.*, lateral pouch ; *l.t.*, lateral tooth ; *m.c.*, mill-chamber ; *m.g.*, mid-gut ; *m.t.*, median tooth ; *o.b.*, opening of bile duct ; *œs.*, œsophagus ; *p.car.*, pterocardiac ossicle ; *p.py.*, prepyloric ossicle ; *py.*, pyloric ossicle ; *u.car.*, urocardiac ossicle ; *v.*, the several pieces of an arrangement of valves which directs the solid residue of the food into the hind-gut, there to become the fæces ; *z.car.*, zygocardiac ossicle.

This consists of two chambers, a large forepart or mill-chamber, or cardiac division of the stomach, and a smaller hind part or filter-chamber, or pyloric division, separated from the mill-chamber by a pit in the roof. From the filter-chamber the short mid-gut or mesenteron leads backwards to the long hind-gut, or ' intestine'. The epidermis and cuticle turn inwards at the mouth and line the gullet and proventriculus, which are together known as the fore-gut. The mid-gut is lined with soft endoderm, and the

hind-gut is again lined with epidermis and cuticle. The cuticle in the gut is for the most part thin, but in places in the proventriculus it forms stout plates or ossicles, certain of which bear strong teeth which project into the forepart of the organ. By the action of muscles these can be brought together to crush the food. The whole apparatus is known as the gastric mill. Into the mid-gut opens on each side a large, lobed, yellow gland, often called liver or hepatopancreas, consisting of numerous short tubes joined by ducts which finally communicate with the mid-gut by an opening on each side. It is, however, much more than a gland, as the finer particles from the fore-gut are directed into it by the filter chamber and are digested in it ; it is best known by the collective name digestive diverticula. The roof of the mid-gut is prolonged into a short blind gut or cæcum. Food is either raked up by the third maxillipeds or seized by the chelipeds and torn up by them and the smaller pincers. It is passed forwards by the jaws to the mouth, where pieces are cut from it by the mandibles and thrust by the mandibular palps and the maxillules into the mouth. It is chewed in the proventriculus, and partially digested by a protease sent forward from the diverticula, before being passed into the diverticula themselves for further digestion and absorption. The cuticle of the gut is shed with that of the body. Shortly before a moult two flat calcareous bodies, known as ' crabs' eyes ' or gastroliths, are laid down in the forepart of the proventriculus. They are ground up before the moult takes place. It is uncertain whether they consist of matter removed from the armour of the body to weaken it in preparation for the moult or are a store of material for the strengthening of the new cuticle. Possibly they serve both purposes.

BLOOD VESSELS

The heart (Fig. 15.8) is a hollow organ with thick, muscular walls. It is roughly hexagonal in outline, as seen from above, and lies in the thorax, above the hind-gut and immediately below the cardiac region of the carapace, in a space, known as the pericardial sinus, with membranous walls, to which the heart is connected by six fibrous bands called the alæ cordis. Three pairs of valved openings or ostia admit blood from the pericardial sinus to the heart : one pair is dorsal, another lateral, and the

third ventral. From the front end of the heart arise three vessels —a median ophthalmic artery, which runs straight forwards over the proventriculus to supply the eyes and other organs of the head, and a pair of antennary arteries, which start one on each side of the ophthalmic, run forwards and outwards, and divide each into two branches, one gastric and the other to the antennæ and green gland. Behind and below the antennaries arise a pair

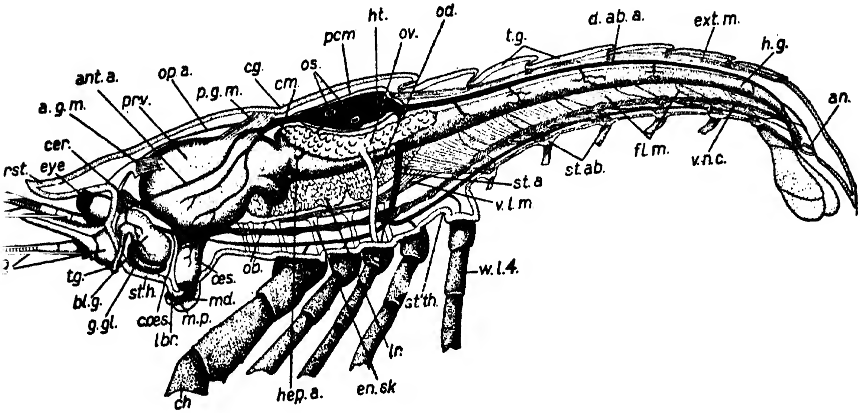


FIG. 15.7.—The internal organs of a female crayfish *in situ*. Slightly diagrammatic.

a.g.m., Anterior gastric muscle; *an.*, anus; *ant.a.*, antennary artery; *at.1*, antennule; *at.2*, antenna; *bl.g.*, bladder of the green gland; *c.g.*, cervical groove; *c.œs.*, circumœsophageal commissure; *cer.*, cerebral ganglion; *ch.*, cheliped; *cm.*, cæcum; *d.ab.a.*, dorsal abdominal artery; *en.sk.*, endophragmal skeleton; *eye*; *ext.m.*, extensor muscles; *fl.m.*, flexor muscles, looping from one sternum to another over *v.l.m.*; *g.gl.*, green gland; *h.g.*, hind-gut; *hep.a.*, hepatic artery; *ht.*, heart; *lr.*, liver; *lbr.*, labrum; *md.*, mandible; *m.p.*, mandibular palp; *o.b.*, opening of bile duct; *od.*, oviduct; *œs.*, œsophagus; *op.a.*, ophthalmic artery; *os.*, ostia; *ov.*, ovary; *p.g.m.*, posterior gastric muscle; *pcm.*, pericardium; *prv.*, proventriculus; *rst.*, rostrum; *st.a.*, sternal artery; *st.ab.*, abdominal sterna; *st.h.*, sternal region of the body in front of the mouth; *st.th.*, thoracic sterna; *t.g.*, tubercle for green gland; *tg.*, terga; *v.l.m.*, ventral longitudinal muscles; *v.n.c.*, ventral nerve cord; *w.l.4*, last walking leg.

of hepatic arteries, which supply the liver, and from the hinder angle of the heart there is given off a vessel that at once divides into a dorsal abdominal artery, which runs backwards above the intestine and supplies it and the muscles of the abdomen, and a sternal artery. This passes downwards, through an opening in the ventral nerve cord, and divides into a backward-running ventral abdominal and a forward-running ventral thoracic artery, by which the limbs are supplied. Each of the arteries branches many times, till it finally gives rise to minute vessels in the organs it supplies, but there are no capillaries.

From these vessels the blood passes into great sinuses which

surround the organs. The largest of these is the perivisceral cavity, but there are also blood spaces in the limbs and elsewhere. The blood from the limbs and a great part of that from the perivisceral cavity is gathered up into a sternal sinus, which lies in a tunnel formed by the endophragmal skeleton and contains the ventral nerve cord and ventral thoracic artery. From this a series of afferent branchial sinuses carries the blood to the gills, where it is oxygenated. From the gills it passes by efferent branchial sinuses to the pericardial sinus. Part of the blood from around the stomach, however, passes on each side into the space between the two sides of the fold of carapace which forms

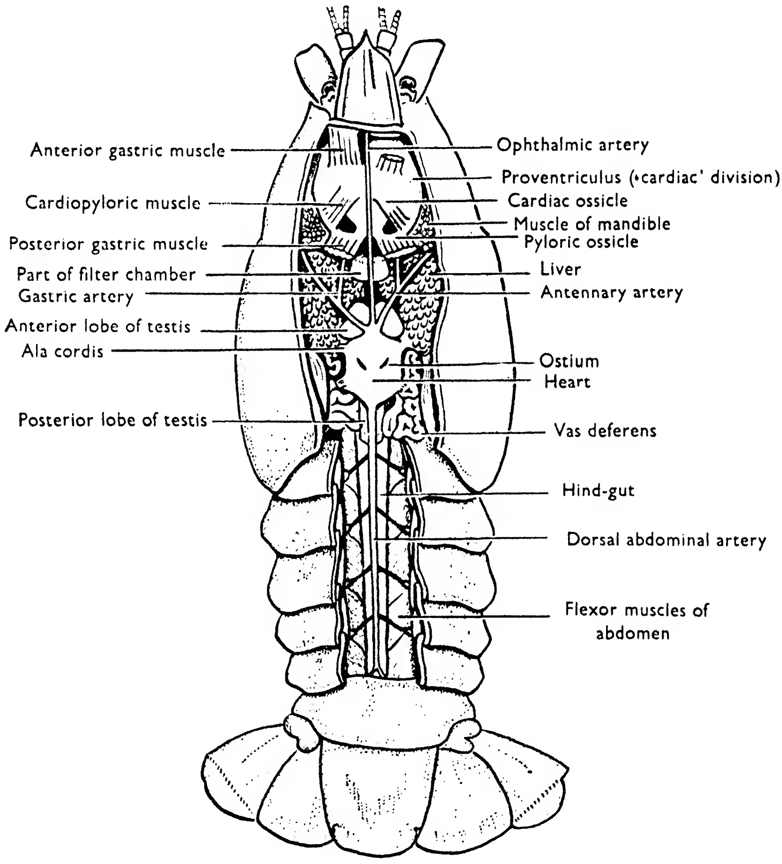


FIG. 15.8.—A male crayfish dissected from the doral surface ; the arteries have been injected.

the branchiostegite, and thence to the pericardial sinus by a vessel which follows the hinder edge of the branchiostegite. It will be noted that the pericardial cavity of the crayfish is a part of the hæmocœle and contains blood, unlike that of the vertebrates, which is a separate part of the cœlom. The blood of the crayfish is

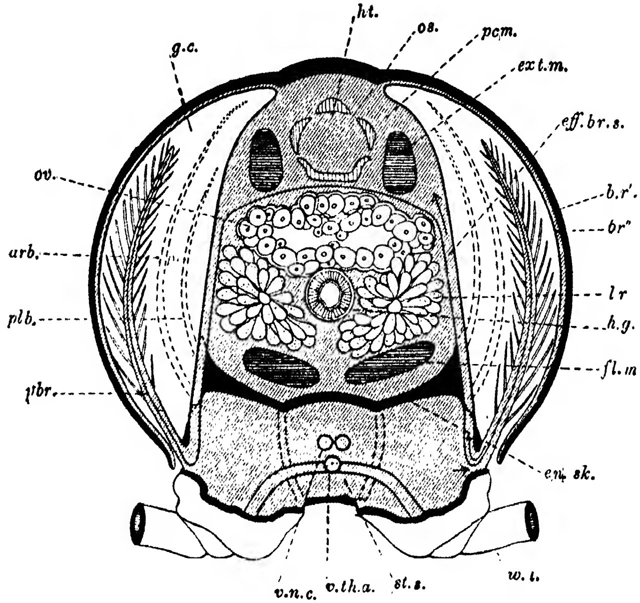


FIG. 15.9.—A diagram of a transverse section through the thorax of a crayfish.

arb., Arthrobranch ; *b.r'.*, outer layer of branchiostegite ; *br"*., inner layer of the same ; *eff.br.s.*, efferent branchial sinus ; *en.sk.*, endophragmal skeleton ; *ext.m.*, extensor muscle of abdomen ; *fl.m.*, flexor muscles of abdomen ; *g.c.*, gill-chamber ; *h.g.*, hind-gut ; *ht.*, heart ; *lr.*, liver ; *os.*, ostia ; *ov.*, ovary ; *pcm.*, pericardium ; *pbr.*, podobranch ; *plb.*, pleurobranch ; *st.s.*, sternal sinus ; *v.n.c.*, ventral nerve cord ; *v.th.a.*, ventral thoracic artery ; *w.l.*, walking leg.

Small arrows in the sinuses on the right-hand side show the course of the circulation of the blood.

a clear fluid, which contains white corpuscles and clots readily—an obvious advantage to an animal whose open vascular system causes it to bleed freely from any wound. A respiratory pigment known as hæmocyanin, which is an organic compound of copper, is dissolved in it, and plays the same part as hæmoglobin, taking up oxygen in the respiratory organs and parting with it to the tissues. In the oxidised condition it is of a blue colour and tinges the blood.

RESPIRATORY ORGANS

The respiratory apparatus of the crayfish is contained in the gill-chambers (Fig. 15.10). The gills (Fig. 15.11) are branched, thin-walled structures, standing upon the coxopodites of the thoracic limbs and the inner wall of the gill-chamber. In them the blood circulates and exchanges its carbon dioxide for the oxygen which is dissolved in the water that is kept flowing through the chamber

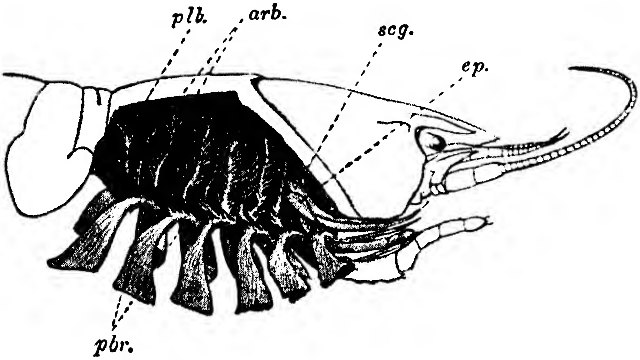


FIG. 15.10.—The forepart of the body of a crayfish, viewed from the right-hand side, with the legs and the branchiostegite cut away and the gills displayed.

arb., Arthrobranchiæ; *ep.*, epipodite of the first maxilliped; *pbr.*, podobranchiæ; *plb.*, pleurobranchia; *scg.*, scaphognathite.

by the action of the second maxilla. This limb is held firm by the curved end of its endopodite, which fits into a groove upon the mandible at the base of the palp, while the exopodite or scaphognathite, flapping at the rate of sixty strokes a minute, bales water forwards, out of the gill-chamber and under the opening of the green gland upon the antenna, so that the excreta is swept away with the foul water from the gills. By this action fresh water is drawn into the chamber between the bases of the legs, and when the oxygen concentration in the water is reduced, the baler flaps faster, so that the supply of oxygen is kept up. No doubt the blood in the branchiostegite is oxygenated through the thin inner wall of that organ.

The gills receive different names according to their position. Those which are attached to the epipodites of the limbs are known as podobranchiæ. Others stand upon the membranes which join

TABLE II

	Maxillipeds.			Legs.					Total.
	I.	II.	III.	I.	II.	III.	IV.	V.	
Podobranchiæ.	Ep	1	1	1	1	1	1	0	6+Ep
Anterior arthrobranchiæ	0	1	1	1	1	1	1	0	6 } 11
Posterior arthrobranchiæ	0	0	1	1	1	1	1	0	5 }
Pleurobranchiæ	0	0	0	0	R	R	R	1	1+3R
Total	Ep	2	3	3	3+R	3+R	3+R	1	18+3R+Ep

Ep=epipodite without a gill. R=abortive rudiment.

the limbs to the body, and are known as arthrobranchiæ, and a few stand upon the inner wall of the gill-chamber (the side wall of the thorax) above the legs, and are known as pleurobranchiæ, the three names being often anglicised by omission of the terminations. The distribution of the gills is shown in Table II.

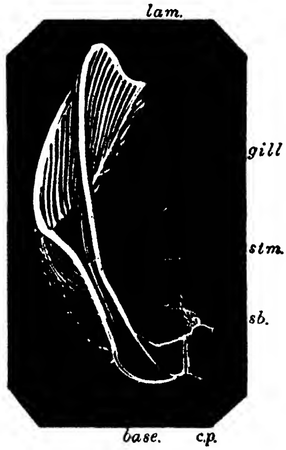


FIG. 15.11.—A podobranch of the crayfish, seen from behind. *Base*; *cp.*, coxopodite; *gill*; *lam.*, lamina; *sb.*, setobranch or tuft of coxopoditic setæ; *stm.*, stem.

Each arthrobranch and pleurobranch has a tree-like structure, consisting of a trunk or axis arising from the body by one end, with numerous short branches or filaments. In the podobranch the axis is fused to the epipodite along the greater part of its length, so that the filaments appear to arise from the epipodite. The tip of the gill, however, stands free. The epipodite is folded along its length, so that a groove is formed, into which fits the gill of the limb next behind.

OSMOTIC REGULATION AND EXCRETION

In the head is a pair of cœlomoducts (p. 188) called antennary or green glands, situated immediately behind the antennæ, upon whose basal joints they open. Each consists (Fig. 15.12) of a

glandular mass and above it a thin-walled bladder from which a short duct leads to the opening. In the centre of the mass is a small, brownish sac, known as the end-sac. The cavity of this is a vestige of the cœlom, which otherwise is in the crayfish represented only by the hollow of the gonad. Partitions project into it from its wall, and it communicates by a small opening with the rest of the mass, known as the labyrinth, which is essentially a winding and much complicated tube leading from the end-sac to the bladder. Its first section, which forms the outer part of the gland, known as the cortex, is greenish in colour and broken into a mesh-work of channels. The rest, the medulla of the gland, is a whitish, coiled tube, simple for a short distance and then made spongy by ridges of its wall. The gland behaves as an osmotic regulator in much the same way as the vertebrate kidney; a filtrate from the blood is first formed, containing its crystalloids but not its proteins, and lower down there is absorption of most ions and secretion of some others. The resulting fluid is of lower concentration than the blood, so that the body gets rid of water. Some nitrogen is lost from the gland but the chief excretory organ is the digestive diverticula. Certain gland cells found on the gills are possibly also excretory. The principal nitrogenous excreta are ammonia and amino compounds.

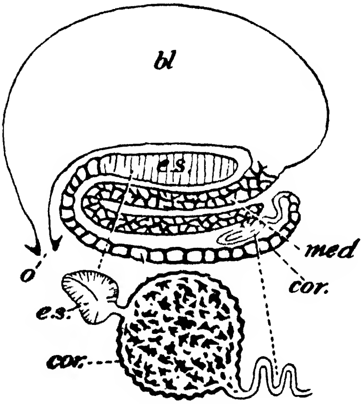


FIG 15.12—A diagram of the structure of the green gland of a crayfish. Above, the whole gland is seem in longitudinal section; below, the end sac and cortex are seen as dissected out and viewed from the surface

bl., Bladder; *cor*, cortex; *e.s*, end sac, *med.*, medulla, *o.*, opening on antenna.

NERVOUS SYSTEM

In its general plan the nervous system of the crayfish resembles that of the earthworm. In the front part of the head, between the green glands, lies a supra-œsophageal or cerebral ganglion, or brain (Fig. 15.13), which corresponds in position to the supra-pharyngeal ganglia of the worm. It gives nerves to the eyes, antennules, and antennæ, and from it two long circumœsophageal

commissures pass backwards to join behind the œsophagus in the subœsophageal ganglion. This gives nerves to the limbs as far as the second maxillipeds, inclusive, and immediately behind it lies the first thoracic ganglion, which supplies the third maxillipeds. In each of the remaining segments of the thorax lies an indistinctly double ganglion which supplies by several nerves the limbs and other organs of its segment. These ganglia are set at some distance apart and are connected by double commissures, forming thus a ventral cord. Between the fourth and fifth ganglia the commissures part widely to allow the sternal artery to pass between them. In the abdomen the cord is continued and consists of a ganglion in each somite united to its fellows by longitudinal commissures, which are really double, but appear at first sight to be single. The last ganglion supplies the telson as well as its own somite. The commissures contain no nerve cell bodies. The brain is more complex than those of annelids and exercises more control over the rest of the nervous system. Giant fibres run from cells in it along the whole length of the cord and enable it to bring about sudden movements which involve distant parts of the body, such as the backward escape movement.

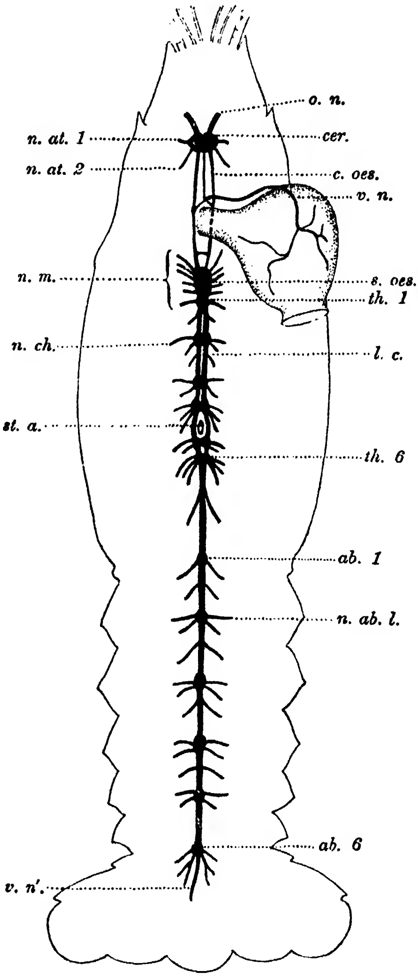


FIG. 15.13.—A semi-diagrammatic view of central nervous system of a crayfish.

*ab.*1, *ab.*6, The first and sixth abdominal ganglia ; *cer.*, cerebral ganglion ; *c.œs.*, circumœsophagea commissure ; *l.c.*, longitudinal commissures of ventral cord ; *n.ab.l.*, nerves to abdominal limbs, *n.at.*1, nerve to antennule ; *n.at.*2, nerve to antenna; *n.ch.*, nerve to cheliped ; *n.m.*, nerves to limbs adjoining the mouth ; *o.n.*, optic nerve ; *s.œs.*, subœsophageal ganglion ; *st.a.*, sternal artery, *th.*1, *th.*6, first and sixth thoracic ganglia ; *v.n.*, nerve to proventriculus ; *v.n'.*, nerve to hind-gut.

A transverse commissure immediately behind the œsophagus joins the two circumœsophageal commissures. It contains fibres which take this roundabout course between the portions of the brain which supply the antennæ, thus indicating that these limbs belong to the same series as those behind the mouth. That is probably also true of the antennules, and the fact that the antennules and antennæ are innervated from the supra-œsophageal ganglia must be connected with the position of the mouth, which, as a result of cephalisation (p. 192) to a high degree is farther back than in the earthworm, where it lies in front of the first somite. The alimentary canal is supplied by two visceral nerves. The first has a three-fold origin, being formed by the junction of a nerve from the cerebral ganglion with two nerves which arise each from a small ganglion on the course of the circumœsophageal commissure. The second arises from the last abdominal ganglion.

SENSE ORGANS

The eyes of the crayfish are compound, containing a number of elements, known as ommatidia, each of which is capable of forming a separate image. The whole eye is black, owing to the presence of pigment in some of its cells, and is covered with a colourless portion of the cuticle known as the cornea, divided into a number of square facets, each of which corresponds to an ommatidium. The structure of an ommatidium is shown in Fig. 15.14. The inner ends of the visual cells are continued into fibres which pass into an optic ganglion in the eyestalk, and from this arises the optic nerve.

In strong light the pigment is spread through the cells so that each ommatidium is isolated, and its corneal facet and refractive bodies combine to form a small image of a portion of the field of view. The separate images are combined to form a mosaic image, which is necessarily erect, of the whole field. In weak light the pigment is retracted, and a single diffuse image is formed by the whole eye. In prawns, and presumably in the crayfish, the movement is controlled by hormones. When separate images are formed a compound eye presumably gives very accurate directional vision, especially to a small point of light. It is this which helps the fixation by which the moth flies towards the candle, turning always so that the same ommatidium is brightly illuminated.

The statocysts (Fig. 15.15) are pair of sacs, situated in the basal

joints of the antennules and provided with nerves. Each has a cuticular lining beset with hairs, with which the nerve fibres

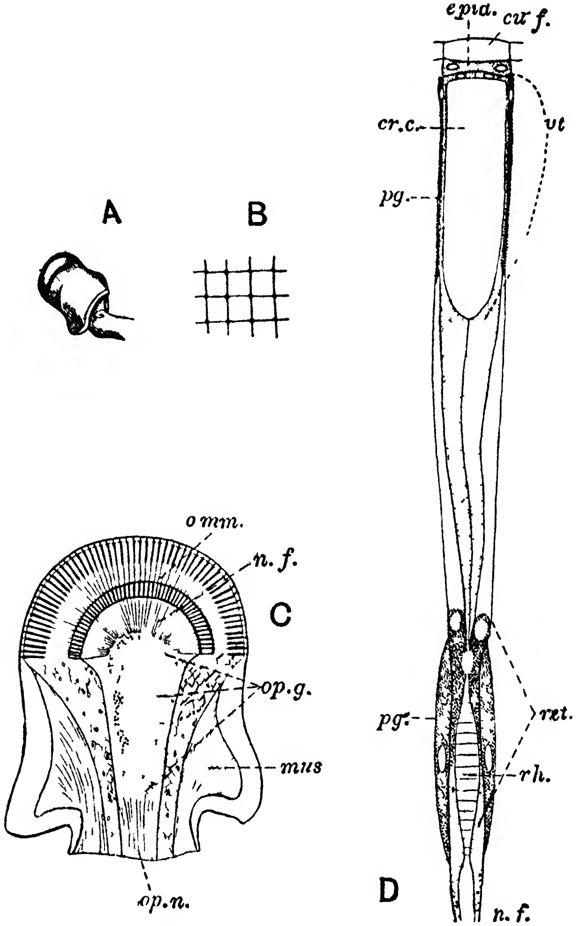


FIG. 15 14.—The eye of the crayfish.

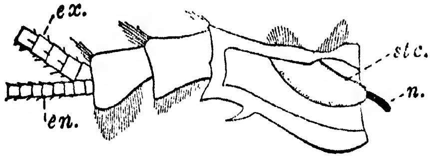
A, The left eye removed; *B*, a portion of the cornea magnified to show the facets; *C*, a longitudinal section of the eye under low magnification; *D*, a single ommatidium highly magnified.—*D* after Parker.

cr.c., Outer refractive body or crystalline cone; *cu.f.*, cuticular facet; *epid.*, epidermis (hypodermis); *mus.*, muscles which move the eye; *n.f.*, nerve fibres; *omm.*, ommatidia; *op.g.*, optic ganglion; *op.n.*, optic nerve; *pg.*, outer pigment cells; *pg'.*, inner pigment cells; *ret.*, retinula cells (the sense cells)—these cells contain pigment; *rh.*, inner refractive body or rhabdome secreted by the retinulæ; *vt.*, vitrellæ or cells which secrete the crystalline cone.

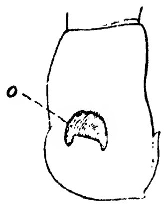
are in communication. Within it are grains of sand, which are scattered over the opening of the sac by the pincers and fall into it. It is probable that the principal function of the organ is informing the animal of its position by the movements of the sand grains

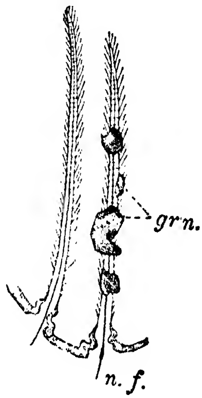
against the hairs, and thus enabling it to keep its equilibrium. If the statocysts be removed, the crayfish loses its sense of position and will often swim upside down. Presumably the sand grains falling to the bottom of the sac by gravity stimulate nerve-

A



B





C

FIG. 15.15.—The statocyst of the crayfish.

A, The right antennule, seen from the median side with the basal joint opened and the flagella cut short ; *B*, basal joint of the left antennule from above ; *C*, two hairs from the statocyst.—*C* partly after Howes.

en., Inner flagellum ; *ex.*, outer flagellum ; *grn.*, sand grains ; *n.*, nerve of the statocyst ; *n.f.*, nerve fibres ; *o.*, opening of the statocyst ; *stc.* statocyst.

endings, so that the necessary muscular movements for the maintenance of position are produced. It has been possible to replace the sand grains in the statocysts of a prawn by iron filings, and the animal can then be induced, by a magnet held above it, to turn over on its back. The antennules bear on their outer flagella bristles which are sensitive to chemical substances. Various of the setæ, especially those of the antennæ, are organs of touch.

REPRODUCTION

The sexes of the crayfish are separate. The generative organs lie in the thorax, above the gut and below the pericardium. They

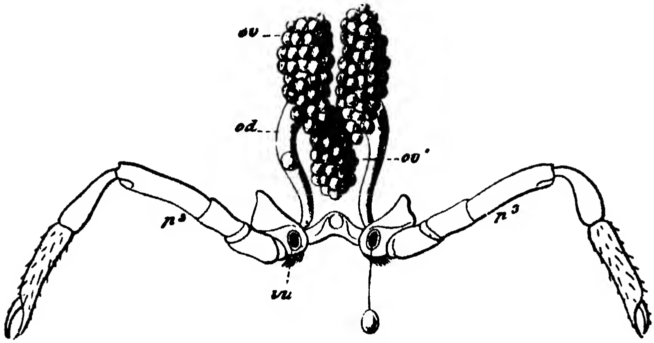


FIG. 15.16.—The reproductive organs of a female crayfish.—After Suckow.
od., Oviduct ; *ov.*, ovaries ; *ov'.*, fused posterior part (median lobe) ; *vu.*, female aperture on the second walking leg (p^3).

have the same general shape in the two sexes, consisting of three lobes, two anterior and one posterior, with a pair of ducts, which start from the junction of the anterior and posterior lobes and run to openings on walking legs. The ovary (Fig. 15.16) is larger and broader than the testis, and has an internal cavity into which the eggs are shed. The oviducts are short, straight, and wide ; they open upon the coxopodites of the second pair of walking legs. The testes (Fig. 15.17) consist of a number of branching ducts which end in small alveoli, in which the spermatozoa are formed. The vasa deferentia are narrow and much coiled ; their first part is very slender and translucent, the second part, which forms most of the duct, is wider and glandular, and a short terminal region has muscular walls which force out the sperm. The spermatozoa (Fig. 15.18) are relatively large discs about 15 microns in diameter, with stiff, pointed processes round the edge. The nucleus is a round capsule and to one side of this is a small,

FIG. 15.17.—The reproductive organs of a male crayfish.—After Huxley.
t., Testes ; *vd.*, vas deferens ; *vd'*, opening of vas deferens on last walking leg.

oval body. Pairing takes place in September and October. The male seizes the female, throws her upon her back, and passes semen through the tubular limbs of his first abdominal segment on to the parts in the neighbourhood of her oviducts, the limbs of his second abdominal pair aiding the process by working to and fro on the hollows of the first. The semen consists of a

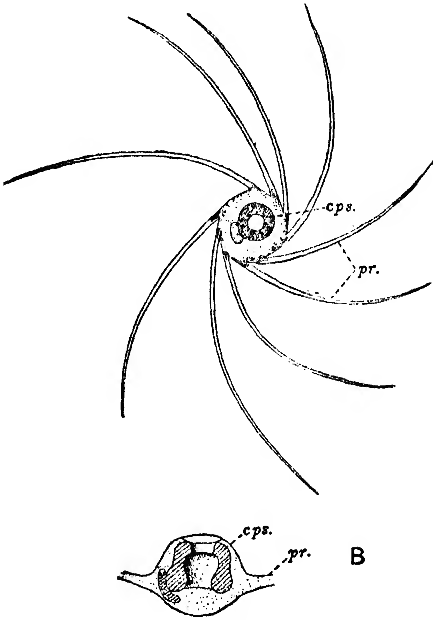


FIG. 15.18.—Spermatozoa of a crayfish.

A Whole spermatozoon from above ; *B*, part, enlarged, in section ; *cps.*, capsule ; *pr.*, stiff processes.

sticky substance, secreted by the vasa deferentia, carrying the spermatozoa, and forms white masses on the sterna of the female. The eggs, which are large and yolky, are laid in November. The processes of the spermatozoa adhere to them, and by a sudden expansion of the contents of the capsule the rest of the body is forced into the ovum. Each egg is attached to one of the hairs on the abdominal limbs by a stalked shell formed of a substance secreted by certain glands on the sterna, and is thus under the protection of the mother during its development. The young are hatched at the beginning of the next summer. They do not differ

greatly from the adult, but have curved tips to the pincers, by which they cling for a time to the empty shell or the abdominal

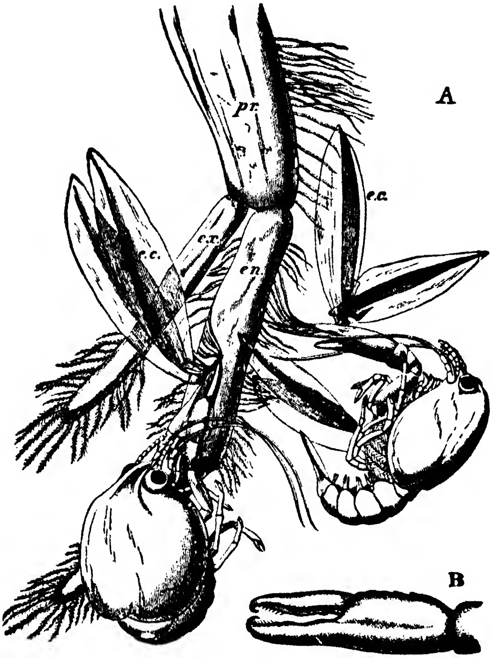


FIG. 15.19.—*A*, Two recently hatched crayfish holding on to one of the swimmerets of the mother ; *B*, pincers of the young more highly magnified.—From Huxley.

e.c., Ruptured egg cases ; *en.*, endopodite ; *ex.*, exopodite ; *pr.*, protopodite.

limbs of the mother (Fig. 15.19), and are thus protected from enemies and kept from being swept away by currents and eventually reaching the sea, where they would perish.

16

COCKROACHES

THE first cockroaches were brought to England, perhaps from the East, in the sixteenth century; they spread slowly, at first but later became ubiquitous; they were of the species *Blatta orientalis*, now known as the common cockroach. In the nineteenth century two other species, *Blattella germanica*, the 'German' cockroach (not a native of the country from which it takes its name), and *Periplaneta americana*, the American cockroach, perhaps from tropical America, were introduced. The first two are found in houses; the third generally only in the larger buildings, such as warehouses and hotels; *P. australasiæ* also occurs, chiefly in glasshouses. The use of DDT as an insecticide has now removed cockroaches from many buildings, and they are difficult to obtain. All cockroaches are nocturnal, and if a light is suddenly switched on they run back to shelter; occasionally one will freeze instead, and is easily caught. They prefer warm places, and are omnivorous, eating not only human food, but paper, hair, and leather. They find their food by smell.

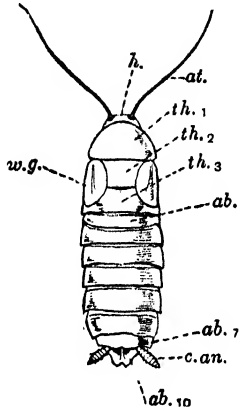


FIG. 16.1.—A female of the common cockroach. The body is somewhat compressed so as to show the membranes between the abdominal terga. The legs have been removed.

ab.1–ab.10, Abdominal terga; *at.*, antenna; *c.an.*, anal cerci; *h.*, head; *th.1*, prothoracic tergum; *th.2*, mesothoracic tergum; *th.3*, metathoracic tergum; *w.g.*, vestige of fore wing.

The simplest way of telling the adults of the three common species is by their wings and their size. *Blatta* is an inch long, *Blatella* a little more than half an inch, and *Periplaneta* an inch and a half. The wings of *Blatella* and *Periplaneta* (which are not likely to be confused) cover the abdomen; those of the male *Blatta* leave three or four segments exposed, and those of the female are vestigial. In the general structure they are alike.

EXTERNAL FEATURES

In its main lines the anatomy of a cockroach resembles that of a crayfish. The animal is segmented, the segments (somites) being unlike and grouped into three regions known as head, thorax, and abdomen, but these do not correspond with the parts similarly named in the crayfish. There is a thick cuticle, not moulted by the adult, and some somites bear jointed limbs. The thorax bears also two pairs of wings. At the sides of the head

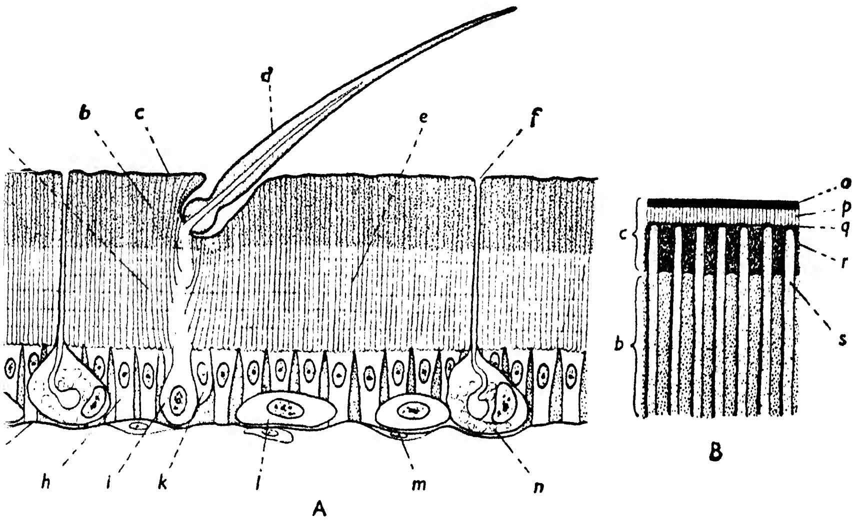


FIG. 16.2.—Insect cuticle.—From Wigglesworth, *Bio. Rev.*, 1948. 23, 408.

A, ideal section of the integument ; *B*, schematic section of the epicuticle.
a, endocuticle ; *b*, exocuticle ; *c*, epicuticle ; *d*, bristle ; *e*, pore canals ; *f*, duct of dermal gland ; *g*, basement membrane ; *h*, epidermal (hypodermal) cell ; *i*, *k*, and *l*, special cells of epidermis ; *m*, blood cell ; *n*, dermal gland ; *o*, cement layer ; *p*, wax layer ; *q*, polyphenol layer ; *r*, cuticulin layer ; *s*, pore canal.

lie a pair of large, unstalked, compound eyes. The cœlom, of which traces are found in development, disappears in the adult, but there is a hæmocœlic perivisceral cavity containing blood.

The insect cuticle is much more than a mere covering of chitin. There are three layers (Fig. 16.2). The innermost and thickest is the endocuticle, which is made of chitin and a protein called arthropodin, intimately associated and perhaps chemically combined. Outside this is the exocuticle ; it has basically the same structure as the endocuticle, but the protein has been tanned, a process which involves both oxidation and the introduction of aromatic groups to the protein molecule. The result is a

substance called sclerotin, which is much harder and less permeable to water than arthropodin, its predecessor. It is sclerotin which has made possible the rigid arthropod exoskeleton, and so, as a special development, insect flight. Outside the exocuticle is a very thin layer, a few microns only, called the epicuticle. It has three main layers but contains no chitin; on the inside a tanned protein called cuticulin, then wax, and on the outside a protective cement which is probably also a tanned protein. Almost all the waterproofing of the insect cuticle is done by the waxy layer of the epicuticle, yet it is never more than a fraction of a micron in thickness. The total thickness of the cuticle in the cockroach is about 40 microns; in many other insects it is much less, and in some, such as the larva of the water beetle *Dytiscus*, much more.

The whole of the cuticle is secreted by the cells of the epidermis (hypodermis); cuticulin first, then the exocuticle, and then the endocuticle. The endo- and exocuticle, and probably the cuticulin of the epicuticle, are at first traversed by vertical pore canals, which contain cytoplasm. When the cuticulin and exocuticle have been formed, a somewhat temporary layer, the polyphenol layer, is spread over the surface, and the waxy layer is next spread over this; presumably both these come through the pore canals. At this point the old skin is shed in ecdysis. The cement layer is almost immediately spread over the surface from the dermal glands, and the hardening of the exocuticle takes place. The endocuticle is continuous with the exocuticle, but is laid down after ecdysis. While the first part of the new cuticle is being secreted, and before ecdysis, a liquid called moulting fluid appears between the new epicuticle and the old endocuticle. It contains a protease and probably a chitinase, and gradually dissolves the old endocuticle, the products being absorbed, through the new cuticle, into the epidermal cells. The exocuticle and epicuticle are not attacked, but as there are lines where no exocuticle has been laid down, the cuticle here becomes reduced to the epicuticle, and so is very thin. It is along these lines that it splits in ecdysis, so that the insect can crawl out of its own skin.

In some insects the pore canals retain their cytoplasm throughout life, and the cuticle is therefore living; in others they become occluded. The various stages of the formation of cuticle, and so the ecdysis, are controlled by hormones secreted by structures called corpora allata, situated just behind the brain.

There is some evidence that the secretion of the hormone is itself determined by events in the outer world, acting via the sense organs and nervous system.

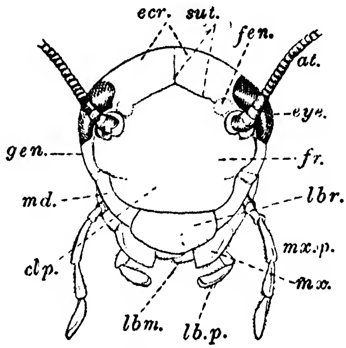


FIG. 16.3.—The head of a cockroach seen from in front.

at., Antenna; *clp.*, clypeus; *ecr.*, epicranium; *eye*; *fen.*, fenestra; *fr.*, frons; *gen.*, gena; *lbm.*, part of the labium; *lb.p.*, labial palp; *lbr.*, labrum; *md.*, mandible, *mx.*, part of the maxilla; *mx.p.*, maxillary palp; *sut.*, sutures.

THE HEAD

The head (Fig. 16.3) is short and deep. Seen from in front it has a pear-shaped outline, with the narrow end downwards. Its armour consists of several pieces—two epicranial plates side by side above, two genæ at the sides below the eyes, a frons and clypeus in front. A labrum is hinged on to the clypeus below; its lining is known as the epipharynx. The appendages of the head are paired, and are shown in Fig. 16.4 and in Table III.

TABLE III

Head Appendages of a Cockroach

Segment	Appendages	Principal Features
1	None	
2	Antennæ	Long, unbranched, many-jointed.
3	None	
4	Mandibles	Strong, toothed; no palps.
5	Maxillæ	Two lobes, and a long palp.
6	Labium	Basal portion of the appendages fused; attached to this on each side are two lobes and a palp.

THORAX

The head is joined by a soft neck to the thorax. This consists of three segments—the prothorax, mesothorax, and metathorax. Each has a tergum or notum above and a sternum below, joined to one another at the sides by membrane in which lie small sclerites—the pleura—which are really basal podomeres of the legs. The pronotum is the largest and projects in front so as to hide the neck. Each sternum bears a pair of legs. The shape of

these legs and the names of their podomeres are shown in Fig. 16.5. The mesothorax and metathorax bear each a pair of wings jointed to the anterior corners of the notum. The wings are membranous folds of the skin, in which the epidermis has practically disappeared and the two layers of cuticle have come together. Branched ridges known as 'veins' or nervures strengthen the wings. The veins are hollow and each contains a trachea (p. 227) and a nerve.

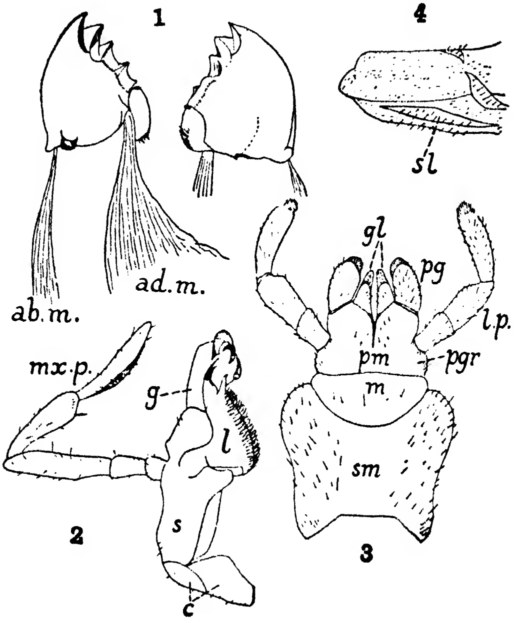


FIG. 16.4.—The mouth-parts of a cockroach.—From Imms.

1, Mandibles; *ab.m.*, *ad.m.*, abductor and adductor muscles; 2, maxilla; *c.*, cardo; *g.*, galea; *l.*, lacinia; *mx.p.*, maxillary palp; *s.*, stipes; 3, labium; *gl.*, glossa; *l.p.*, labial palp; *m.*, mentum; *pg.*, paraglossa; *pgr.*, palpiger; *pm.*, prementum; *sm.*, submentum; 4, hypopharynx; *sl.*, left vestigial superlingua.

The first pair of wings are dark-coloured and tough (the tegmina) and form a cover for the second, which, when they are at rest, are folded lengthwise and laid along the back. In the female of *B. orientalis* the wings are very small. Wings are not appendages of the same kind as the limbs, but movable expansions of the terga.

ABDOMEN

The abdomen consists of ten somites, each with a tergum and a sternum, joined at the sides by soft cuticle. The hinder somites are telescoped, so that the eighth and ninth are hidden, except

that in the male *B. orientalis*, portions of the terga remain uncovered. The first sternum is rudimentary, and the tenth tergum projects backwards as a plate with a deep notch in its hinder edge. A pair of many-jointed, spindle-shaped anal cerci, which may represent limbs, are attached under this plate, and below it is the anus, between two podical plates or paraprocts, which may represent the sternum of an eleventh somite. In the female the seventh sternum is produced backwards into a large boat-shaped process, which forms the floor of a genital pouch, and in the male the ninth sternum bears a pair of limbs in the form of

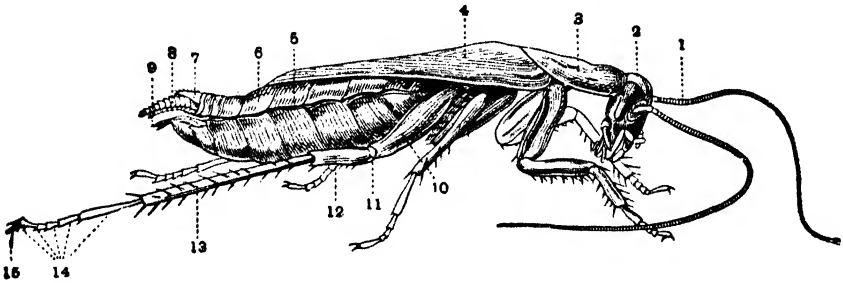


FIG. 16.5.—A male of the common cockroach (*P. orientalis*) in side view.—From Shipley and MacBride.

1, Antenna; 2, head; 3, prothorax; 4, fore wing; 5, soft skin between terga and sterna; 6, sixth abdominal tergum; 7, split portion of tenth abdominal tergum; 8, anal cerci; 9, styles; 10, coxa of third leg; 11, trochanter; 12, femur; 13, tibia; 14, tarsus; 15, claws.

slender, unjointed styles. The genital opening is placed below the anus and is surrounded by a complicated set of processes known as gonapophyses. A pair of stink glands, deterrent to most enemies, opens on the membrane between the fifth and sixth terga. Segments one to eight are limbless.

LOCOMOTION

While the insect is walking, three legs are in contact with the ground at one time. On one side the first leg pulls and the third pushes while on the opposite side the second leg acts as a prop. Meanwhile the other three legs are being moved forwards to repeat the process.

In flight, the hind wings beat in a complicated figure which both supports the body and drives it forwards. They are moved by two sets of muscles—an indirect set, consisting of vertical and longitudinal muscles of the thorax which by alternately

lowering and raising the tergum, to which the wings are attached, lever the wings up and down upon the side plates (pleura) upon which they rest (Fig. 16.8), and a direct set attached to the base of each wing, which they can both rotate upon its axis and extend from the body or retract. The hind-wings are beaten down and up, and at each downstroke the strong front edge (costa) is by muscular action rotated downwards and forwards so that the somewhat concave lower surface faces obliquely downwards and backwards. This process is assisted by the

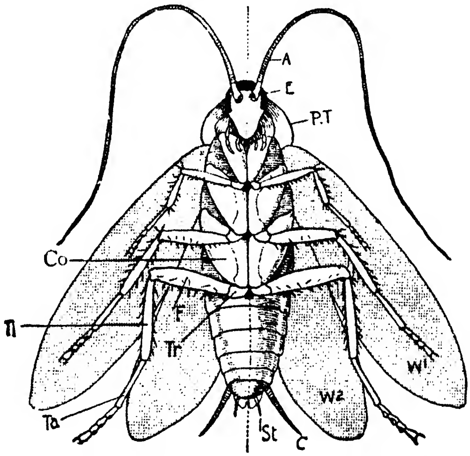


FIG. 16.6.—The ventral aspect of a male American cockroach with the wings extended. An imaginary median line has been inserted.—From Thomson.

A, Antennæ; *C*, cercus; *Co*, coxa, the breadth of which makes it look, in its present position, like a ventral plate on the body; *E*, eye; *F*, femur; *P.T*, prothorax; *St*, style; *Ta*, tarsus; *Ti*, tibia; *Tr*, trochanter; W^1, first pair of wings; W^2, second pair of wings.

resistance of the air below bending the thin hinder part of the wing upward. As a result, during the beat the wing exerts pressure both downwards and backwards while a region of decreased pressure is created above and in front of it. Thus the insect is pressed and drawn upwards and forwards. The forewings are held at right angles to the body, but do not beat.

BODY CAVITY AND ALIMENTARY SYSTEM

The body cavity of an insect, which like that of the crayfish is a hæmocœle, is divided into two parts. The upper is the pericardium, and below this is the perivisceral cavity through which passes the gut. Most of the space of both parts is filled by the fat

body (Fig. 16.7), some of whose cells hold reserves of fats, carbohydrates and proteins, others contain uric acid, and some have bacteria which may be symbiotic.

The alimentary canal (Fig. 16.9) has long, ectodermal fore- and hind-guts, lined with cuticle as in the crayfish. The fore-gut comprises (i) the mouth, which is divided into an anterior (morphologically dorsal) and a posterior (morphologically ventral) chamber by a vertical tongue-like hypopharynx ; (ii) the narrow gullet, lying in the neck ; (iii) the swollen crop ; (iv) the proventriculus or gizzard, which has muscular walls and contains six hard, cuticular teeth and some pads covered with bristles which form a strainer. Two diffuse labial or salivary glands lie on each side of the crop, and between each pair lies a salivary bladder or receptacle. The ducts of the two glands of each side join ; the common ducts of the two sides then unite to form a median tube, and this is joined by another median tube formed by the union of the ducts of the receptacles. The final opening is at the base of the posterior surface of the hypopharynx. The mid-gut or mesenteron, lined by soft endoderm, is short and narrow and bears at its beginning seven or eight club-shaped pyloric cæca. The gizzard projects funnel-wise into the mid-gut. The hind-gut is coiled and divided into a narrow ileum, a wider colon, and a wide rectum, which has six internal ridges. At the beginning of the hind-gut are attached a number of long, fine Malpighian tubules the epithelium of which is excretory.

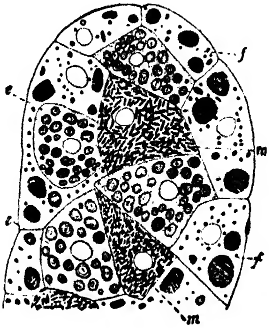


FIG. 16.7.—A section through a lobe of the fat body of a cockroach × 650.—From Imms.

e, Excretory cell with concretions ; *f*., fat cell ; *m*.. cell containing bacteria.

DIGESTION AND EXCRETION

The food is cut up by the mandibles and maxillæ, moistened with saliva, and pushed by maxillæ and labium into the mouth ; it is held up for a time in the crop, where it is acted upon by the saliva, which digests only starch, and by the mid-gut secretion which leaks forward and digests fat. Most of the crop digestion is by yeasts and bacteria which are subsequently themselves

digested by their host. The food is then admitted, little by little, into the gizzard and there broken up fine by the teeth and strained by the bristles as it passes into the mid-gut. The juice secreted here digests all classes of food stuffs: it is secreted

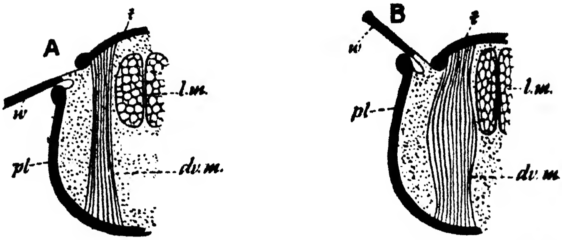


FIG. 16.8.—A diagram to show how the wings of an insect are lowered and raised in flight.

A, The downstroke: the tergum (*t*) is raised, owing to being arched fore and aft by the contraction of the longitudinal muscles (*l.m.*); this forces the wing (*w.*) down, pivoting over a point on the pleuron (*pl.*). *B*, the upstroke: the tergum is lowered by contraction of the dorso-ventral muscles (*dv.m.*); this levers the wing up.

by the break-up of epithelial cells, which are replaced from reserve cells. The delicate, uncuticulate epithelium is protected from hard particles not, like that of backboned animals, by the

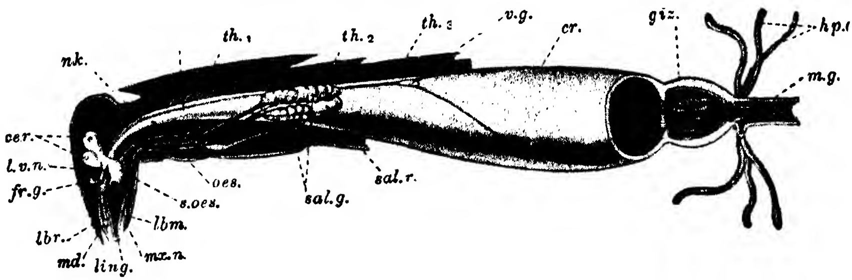


FIG. 16.9.—A semi-diagrammatic drawing of the head and thorax of a cockroach, dissected from the left side.

cer., Cerebral ganglion; *cr.*, crop; *fr.g.*, frontal ganglion; *giz.*, gizzard; *hp.c.*, hepatic cæca; *l.v.n.*, left visceral nerve leaving the brain; *lbm.*, labium; *ling.*, hypopharynx; *lbr.*, labrum; *m.g.*, mesenteron; *md.*, mandible; *mx.n.*, maxillary nerve; *nk.*, neck; *œs.*, œsophagus; *s.œs.*, subœsophageal ganglion; *sal.g.*, salivary gland; *sal.r.*, salivary receptacle; *th.1*, *th.2*, *th.3*, segments of the thorax; *v.g.*, visceral ganglion; *v.n.*, visceral nerve.

secretion of mucus (p. 512), but by a very delicate chitinous envelope, the peritrophic membrane, which is secreted by the epithelium but adheres to it only around the entrance from the gizzard. This membrane is permeable both to digestive enzymes and to digested food. It is in the mid-gut that absorption mainly takes place. The pyloric cæca are mere extensions of the mid-gut and do not differ from it in function. In the hind-gut water is

absorbed both from the fæces and from the urine excreted by the Malpighian tubules. Nitrogen is excreted as uric acid. In most insects some is got rid of by the Malpighian tubules and some laid up in the fat body (see p. 224), but the cockroach appears not to eliminate nitrogen in the urine.

RESPIRATORY ORGANS

The respiratory system consists of branching tubes or tracheæ (Fig. 16.10), of ectodermal origin with a spirally thickened lining of cuticle, which arise from ten pairs of openings, called spiracles or stigmata, at the sides of the body. There are two large spiracles on each side of the thorax, one between prothorax and mesothorax, one between mesothorax and metathorax, and in each of the first eight abdominal somites a spiracle is placed on each side between the tergum and the sternum. There are six main longitudinal tracheæ, two dorsal, two ventral and two lateral, and from there branches divide and subdivide until they end in tracheoles, which have no cuticular lining, ramify in the tissues, and end upon or actually in the cells (Figs. 16.11, 16.12).

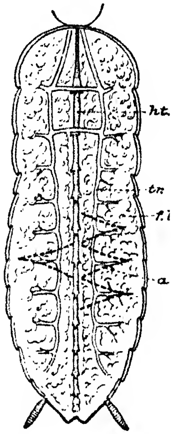


FIG. 16.10.—The heart and neighbouring structures of a cockroach; somewhat diagrammatic.

a.m., Areas marked by dotted lines to show the position of alary muscles below the fatty body; *f.b.*, fatty body; *ht.*, heart; *tr.*, tracheæ.

Movements of the abdomen, combined with opening and closing of the spiracles, pump air in and out of the larger tracheæ, and diffusion makes for further mixing. When the insect is at rest the ends of the tracheoles are full of fluid. When the muscles are active, products of their metabolism raise the osmotic pressure in the tissues, this withdraws the fluid so that air extends more deeply into the tracheoles and reaches their cells (Fig. 16.12). While some carbon dioxide is lost through the tracheal system most diffuses directly through the skin.

BLOOD VESSELS

The direct supply of air to the tissues is no doubt the reason for the simple condition of the blood-vascular system, which

consists of a long heart (Fig. 16.10), lying along the mid-dorsal line of the abdomen and thorax, an anterior aorta, small paired segmental arteries in the mesothorax and metathorax and in abdominal segments 3–6, and a system of ill-defined sinuses, of which the principal is the perivisceral cavity. The heart is enclosed in a pericardial space and is divided into thirteen chambers corresponding to the segments. Each chamber communicates by a pair of ostia at its sides with the pericardial space. Blood from outlying parts of the body flows to the perivisceral cavity, thence into the pericardial cavity through openings in the floor of the latter, and so through the ostia into the heart, which, contracting from behind forwards, drives it through the aorta into the sinus system, by way of the sinuses of the head. Paired triangular alary muscles, whose outer ends are attached to the terga, support the heart. The blood resembles that of the crayfish but, as might be expected in view of the mode of respiration, contains no respiratory pigment.

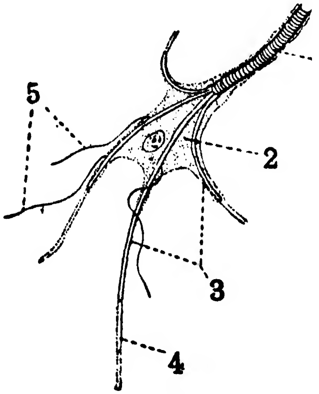


FIG. 16.11.—Detail of tracheal ending. 1, trachea ; 2, tracheal cell ; 3, main tracheoles containing air ; 4, main tracheoles containing liquid ; 5, fine tracheoles containing air. (After Wigglesworth.)—From Yapp, *An Introduction to Animal Physiology*, 2nd edition, 1960. Clarendon Press, Oxford.

NERVOUS SYSTEM AND SENSE ORGANS

The nervous system (Fig. 16.13) is on the same general plan as that of the crayfish. It comprises a pair of supra-œsophageal ganglia, which receive optic and antennary nerves, a pair of short, wide circumœsophageal commissures, a subœsophageal ganglion, and a double ventral cord with a ganglion in each of the first nine segments behind the head. In many insects, especially the Hymenoptera (p. 260), the supra-œsophageal ganglia, which represent three pairs of ganglia fused together, are highly developed and deserve the name brain. The alimentary canal is supplied by a visceral nervous system which receives nerves from the circumœsophageal commissures and the brain. Its principal ganglion lies on the upper side of the crop. The sense organs include the large compound eyes, which resemble

those of the crayfish in structure, the antennæ, which are tactile gustatory and olfactory, the labial and maxillary palps, which are gustatory and olfactory, and anal cerci, which are tactile and also sensitive to sound vibrations, various sensory bristles, and possibly a pair of oval white patches which are found above the bases of the antennæ and are known as the fenestræ.

ORGANS OF REPRODUCTION

The sexes are separate. The testes (Fig. 16.14) are small, paired organs, embedded in the fat body below the fifth and sixth

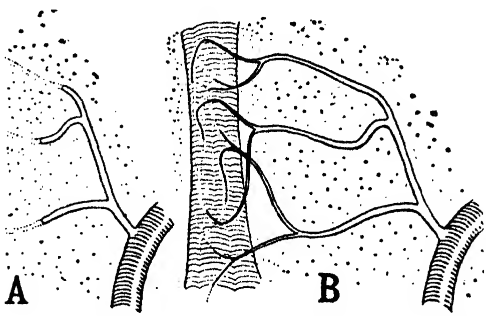


FIG. 16.12.—Tracheoles running to a muscle fibre.—From Imms, after Wigglesworth.

A, Muscle at rest; the terminal parts of the tracheoles (shown dotted) contain fluid; *B*, muscle fatigued air extends far into the tracheoles.

abdominal terga. In the adult the testes are no longer functional. Two vasa deferentia lead backwards and downwards from them to the seminal vesicles, which are beset with short finger-like processes and lie side by side to form the so-called mushroom-shaped gland. The seminal vesicles join behind to form a muscular tube, the ejaculatory duct, which opens by a median pore between the ninth and tenth abdominal sterna. A gland of doubtful function, known as the conglobate gland, lies below the ejaculatory duct and opens with it. The ovaries (Fig. 16.15) are paired organs in the hinder part of the abdomen, each consisting of eight tapering tubes, which show swellings corresponding to ova. There is a single, short, wide oviduct which opens on the eighth abdominal sternum. On the ninth sternum a pair of branched colleterial glands pour out by two openings a secretion which forms the cases of the egg-capsules. There is an unequal pair of spermathecæ, which open between the eighth and ninth

abdominal sterna and store spermatozoa received from a male in copulation. The eggs are produced alternately by the two ovaries, and as they pass down the oviduct are enclosed in a single

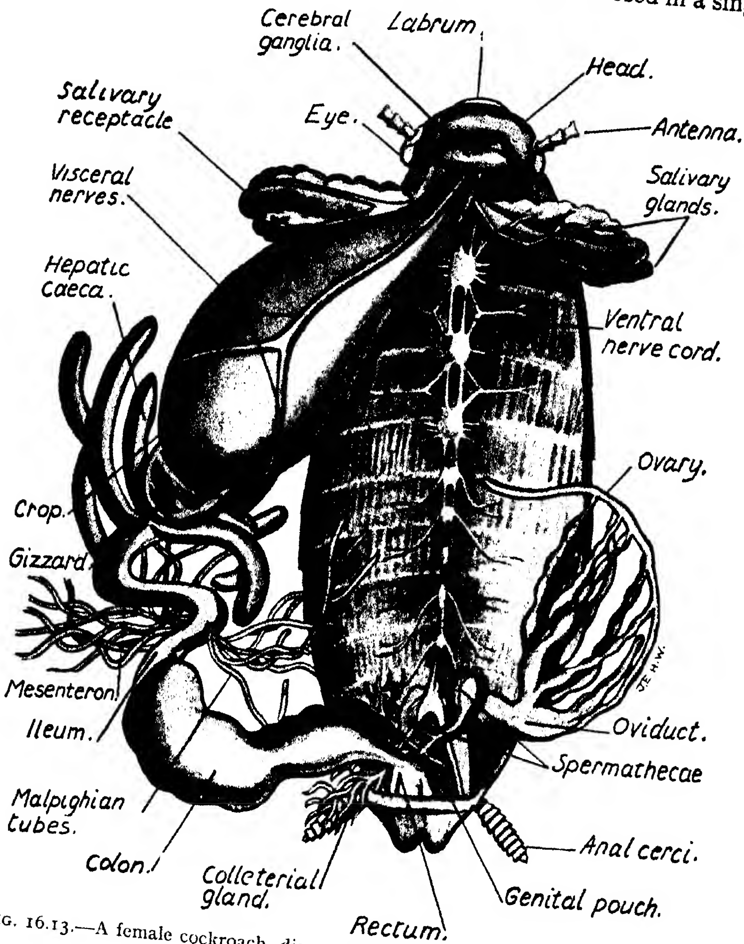


FIG. 16.13.—A female cockroach, dissected from above.—Adapted from Shipley and MacBride.

capsule or ootheca. As more eggs are formed this protrudes from the genital opening, and is finally deposited. One female lays several capsules, and breeding goes on throughout the year. The number of eggs in a capsule varies; in *Blatta orientalis* it is about 16; in *Blatella germanica* about 40; and in *Periplaneta*

americana about 20. Parthenogenesis occasionally occurs. When the eggs hatch the capsule splits and the young emerge. The time

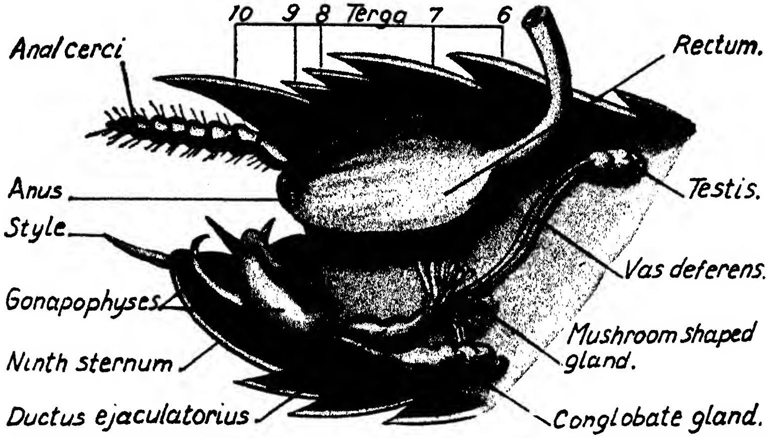


FIG. 16.14.—A semi-diagrammatic view of the hinder part of the body of a male *P. americana* dissected from the right side to show the generative organs.

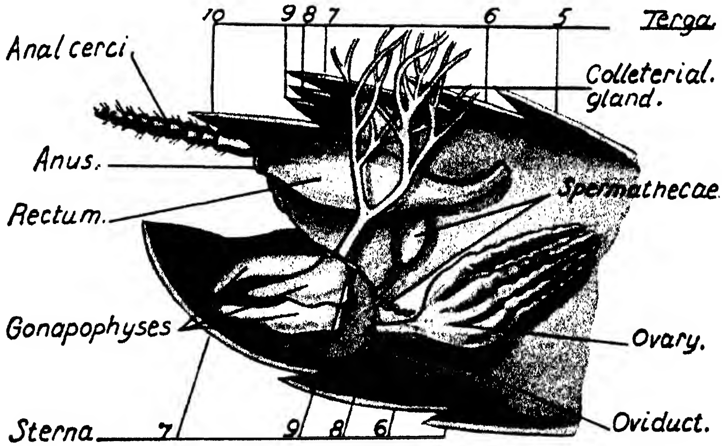


FIG. 16.15.—A semi-diagrammatic view of the hinder part of the body of a female *P. americana* dissected from the right side to show the generative organs.

taken to reach sexual maturity varies with the species, and depends much on external factors such as food and temperature; an average time from egg to imago in the common cockroach is a year or a little less. This species has seven moults, but in no cockroach is there a true metamorphosis (pp. 244–6).

17

ARTHROPODS AND INSECTS

ARTHROPODA

The phylum Arthropoda, to which the crayfish and cockroach belong, is not easy to characterise. Its members resemble the Annelida in being bilaterally symmetrical triploblastic segmented Metazoa, in the general plan of the nervous system, and in the possession of cœlomoducts. They differ in the great reduction of the cœlom and parallel development of a perivisceral hæmocœle, in the absence of nephridia, in the absence (except for *Peripatus*) of cilia and in the totally distinct type of development of the egg (pp. 680–1). As positive features they possess paired jointed limbs, of which at least one pair serves as jaws, and a continuous thickened chitinous cuticle. The classification of the phylum has always been difficult, on account of the vast number of species which it includes, and a recent view is that it is an unnatural assemblage, containing at least three groups of animals which have independently evolved the characters of ' arthropodisation ' from a hypothetical pre-annelid ancestor. The evidence for this is derived partly from palæontology, and partly from a study of structures such as tracheæ, Malpighian tubules, and the jointed legs, which, however similar they may appear, are so different in detail in the different groups that they cannot be homologous. The same is probably true of the compound eyes. Pending general acceptance of this view, and agreed names for what would then become three new phyla, the grouping is indicated in the classification that follows, and the main divisions are shown as subphyla instead of classes, which makes the handling of smaller divisions easier.

GROUP A

SUBPHYLUM I—CRUSTACEA

These are typical arthropods, nearly all aquatic in habit, so that respiratory organs, if present at all, are usually gills. There are two pairs of antennæ, on the second and third somites, and on the fourth somite there is a pair of mandibles. The limbs, of

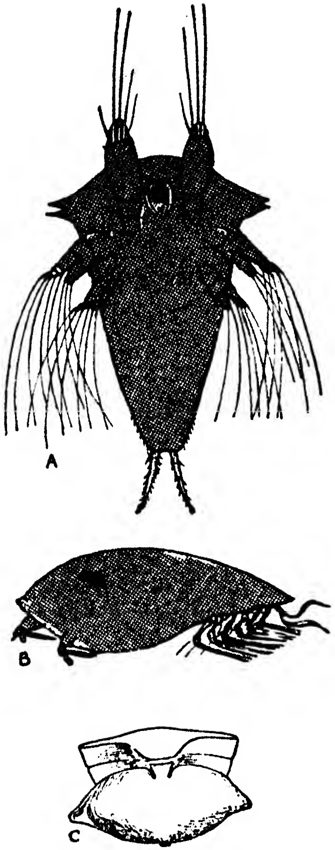


FIG. 17.1.—Development of *Sacculina*.—After Delage. (Not drawn to scale.)

A, Free-swimming nauplius, with three pairs of appendages ; *B*, pupa stage ; *C*, adult protruding from the abdomen of a crab.

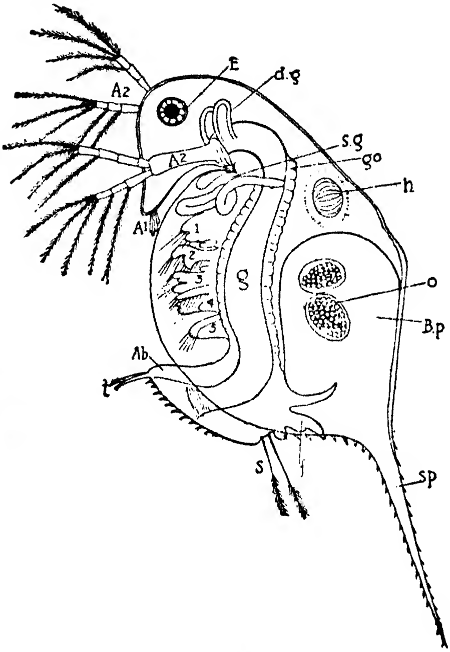
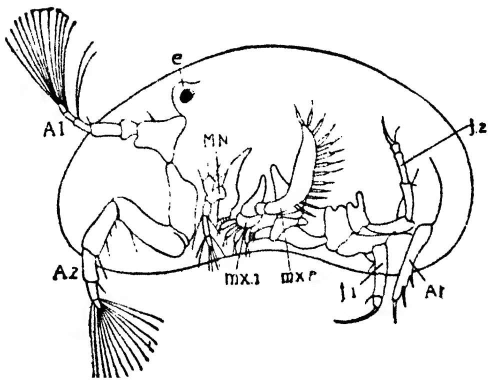


FIG. 17.2.—*Daphnia.*

A^1, first antenna ; A^2, second antenna ; *Ab.*, rudimentary Abdomen ; *B.p.*, brood-pouch ; *dg.*, digestive cæca ; *E.* eye ; *f.*, furca ; *g.*, gut ; *go.*, gonad ; *h.*, heart in pericardium ; *o.*, ovum ; *s.*, setæ ; *s.g.*, shell gland ; *sp.* spine ; *t.*, caudal fork ; 1-5, thoracic limbs.

FIG. 17.3.—*Cypris*, side view, after removal of one valve. —After Zenker.

A1, First antennæ ; *A2*, second antennæ ; *Ab*, rudimentary abdomen ; *e.*, eye ; *f1*, *f2*, thoracic legs ; *MN*, mandibles ; *mx1*, first maxilla ; *mx2*, second maxilla.



which there is usually a fairly complete series, are reducible to a type with two rami. There are not more than two pairs of cœlomoducts, both in the head.

The typical larva is the characteristic nauplius, unsegmented, but with three pairs of appendages and a median eye (Fig. 17.1) The nauplius is however often absent or modified, while there may be other quite different types of larvæ.

The crayfish, which has already been described as a type,

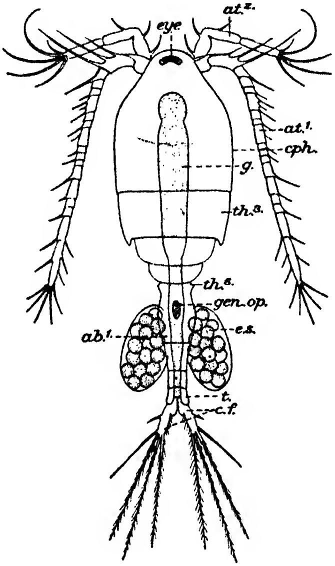


FIG. 17.4.—*Cyclops.*

*ab.*1, First abdominal segment; *at.*1, antennule; *at.*2, antenna; *c.f.*, caudal fork; *cph.*, cephalothorax (fused head and first two thoracic segments); *e.s.*, egg sac; *eye* (single and median); *g.*, alimentary canal; *gen.op.*, genital opening; *t.*, telson; *th.*3, *th.*6, third and sixth thoracic segments.

In comparing this crustacean with the crayfish, note the absence of proventriculus, paired eyes, uropods, and carapace, the presence of median eye and caudal fork, and the difference in the number of segments.

belongs to the most highly developed class, the Malacostraca, the most prominent features of which are the stalked compound eyes and the large carapace covering the thorax. This class includes the lobsters, crabs, prawns, and shrimps, and also the best-known terrestrial Crustacea, the woodlice of the Order Isopoda. Other classes are the Branchiopoda, characterised by flat abdominal appendages (phyllopodia), e.g. *Daphnia*, the water flea; the Ostracoda, with a bivalve carapace, e.g. the freshwater *Cypris*; the Copepoda, with no abdominal appendages,

which include the free-living freshwater *Cyclops*, and a number of interesting parasites such as *Argulus*, the carp louse ; and the Cirripedia, which are sedentary when adult and include the barnacles such as *Lepas* and *Balanus*, and extreme parasites such as *Sacculina*, which, living partly attached to the underside of the intestine of a crab, and partly beneath its abdomen, sends suckers which penetrate throughout the body of its host. The Cirripedia are scarcely recognisable as Crustacea apart from their larval forms, which are more or less normal.

GROUP B

SUBPHYLUM II—TRILOBITA

These are extinct forms, from the Palæozoic era (p. 721).

SUBPHYLUM III—CHELICERATA OR ARACHNIDA

The body is divided into a prosoma of six somites, with appendages of which four pairs are legs and none is an antenna or mandible, and an opisthosoma of thirteen or fewer somites which are often without appendages. The eighth segment bears the genital opening, and the anterior part of the opisthosoma bears respiratory openings of various types, including sometimes the openings of tracheæ. Traces of cœlomoducts are present, sometimes functional as excretory organs or genital ducts, as in the scorpions. The development is nearly always direct.

Most modern arachnids are terrestrial, and the best-known forms in Britain are the class Araneida or spiders (Fig. 17.5). Here the opisthosoma is large and sharply marked off from the prosoma by a waist ; it has lost its segmentation and bears spinnerets, which are transformed appendages, for guiding the silk which is prepared by various glands. The first appendages are subchelate cheliceræ, and the second or pedipalps are modified in the male to take up the semen which he has discharged on to a leaf, and convey it into the genital opening of the female. Respiration is by lung-books, vascular plates situated in pockets on the opisthosoma, and tracheæ (Fig. 17.6). Apart from their web-spinning, the most interesting thing about the spiders is their strongly proteolytic external digestion ; all but the chitin of a fly is dissolved by saliva which is injected into its body, and only liquid is taken into the spider's mouth.

Other arachnid classes are the Scorpionidea or scorpions, with the opisthosoma divided into meso- and meta-soma; the Acarina, or mites and ticks, and the Phalangida or harvestmen, with

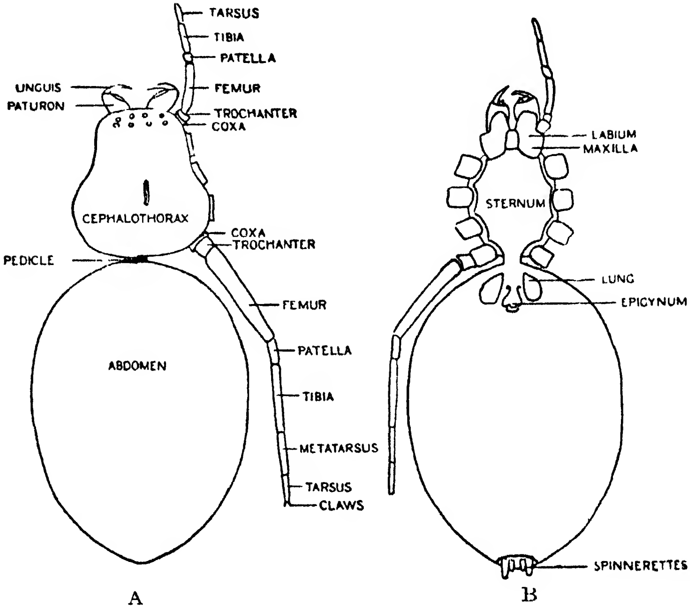


FIG 17 5—Dorsal (A) and ventral (B) surfaces of spider The 'maxilla', or gnathobase of the pedipalp, is not homologous with the maxilla of other arthropods - From Savory, *British Spiders* 1926 Clarendon Press, Oxford

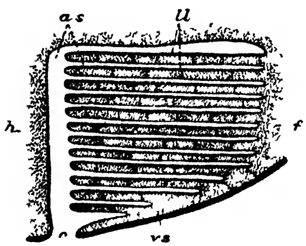


FIG. 17 6—A diagram of a vertical, longitudinal section through a lung-book

a s, Air space, *f*, anterior end *h*, hinder end, *ll*, 'leaves' of book in which the blood flows, *o* opening, on *v s* ventral surface of body.

greatly elongated legs. Many of the Acarina are blood-sucking ectoparasites of man or his domestic animals, important because of the diseases which they carry; the ticks *Ornithodorus moubata* on man and *Boophilus annulatus* on cattle carry relapsing and Texas fever respectively, both fever diseases being caused by spirochætes. The mites *Demodex folliculorum* (Fig. 17.9) which lives in the sebaceous glands, and *Sarcoptes scabiei* (Fig. 17.10), causing the itch, are ectoparasites of man which may produce nothing more than irritation.

GROUP C

SUBPHYLUM IV—ONYCHOPHORA

There are two genera, *Peripatus* (Fig. 17.7) and *Peripatopsis*. They are aberrant forms, possibly not strictly arthropods at all, possessing tracheæ and cilia, and without either thick cuticle or jointed limbs.

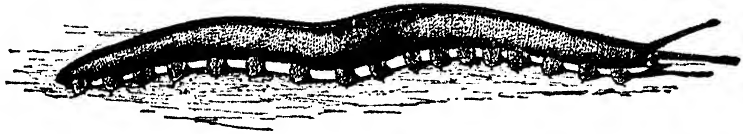


FIG. 17.7.—*Peripatus capensis*, slightly enlarged.—From Borradaile, after Sedgwick. Borradaile and Potts, *The Invertebrata*, 2nd edition, 1935. Cambridge University Press.

SUBPHYLUM V—MYRIAPODA

These are terrestrial, and possess tracheæ ; there is a head with one pair of antennæ, and many segments and legs. They include two classes, which are not very closely related ; the Chilopoda or centipedes, which are carnivorous, with a flattened body and one pair of legs on each segment, and the Diplopoda or millepedes, which are herbivorous, with a cylindrical body and two pairs of legs on each apparent segment, which has been formed by the fusion of two somites.

SUBPHYLUM VI—INSECTA

THE number of different species of insect is enormous, probably not less than 500,000 and equal to that of all other animals put together. All insects resemble the cockroach in the main features of their anatomy, but many of them depart widely from it in detail, the differences affecting principally the mouth-parts, the wings and the life-history.

MOUTH-PARTS

The full set of mouth-parts consists of three pairs of appendages and three median structures. Segment four bears mandibles, segment five maxillæ, and segment six the labium. The median

structures above the mouth are the labrum, which is the most anterior dorsal chitinous plate of the head and is capable of some movement, and the epipharynx, which is the membranous roof of the buccal cavity, often produced outwards and associated

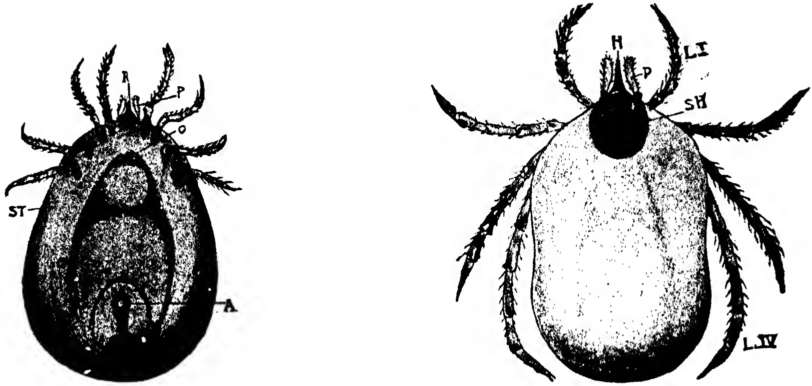


FIG. 17.8.—The sheep tick (*Ixodes ricinus*) female, ventral surface on left, dorsal on right.

A, anus ; *G*, genital aperture ; *H*, hypostome ; *L.I*, *L.IV*, first and fourth legs ; *P*, palp ; *R*, rostrum ; *SH*, oval shield ; *ST*, stigma.—After Wheler.

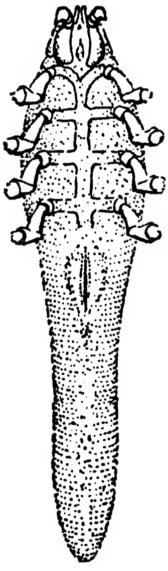


FIG. 17.9.—The follicle mite (*Demodex folliculorum*), in ventral view. —From Thomson.

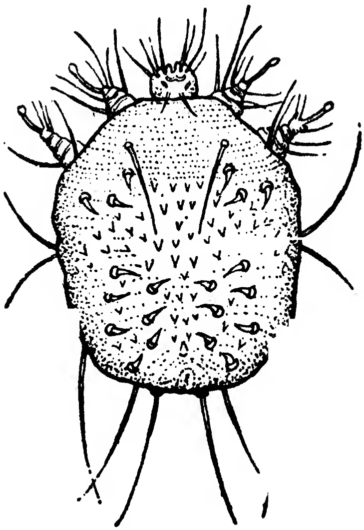


FIG. 17.10.—The itch mite (*Sarcoptes scabiei*), in dorsal view. The two hinder pairs of legs are hidden under the body.—From Thomson.

with the labrum. Below the mouth is the hypopharynx or lingua, which is a median process from the floor of the buccal cavity, and bears the opening of the common salivary duct. The cockroach mouth-parts, which have already been described, have all these parts, and their only important development is the fusion of the basal portions of the labium to form the mentum, which is common to all existing insects which possess the appendage at all. The submentum is probably derived from the wall of the head. Mouth-parts like these, with strong crushing mandibles, are called mandibulate, and are characteristic of the more primitive orders of insects ; they are also found in some members of more advanced groups, especially in the larval stages. Besides the cockroach and its relatives, other important insects which possess them are the grasshoppers, dragonflies, beetles, and saw-flies.

From this full and primitive set of mouth-parts adaptive radiation (p. 474) has gone on in several directions to produce structures suitable for different types of food. Often the same end is reached by more than one means ; there are, for example, several different modifications for sucking liquid food. On the whole, where the mandibles are well developed the maxillæ are primitive, and parts of the maxillæ which are large have small counterparts in the labium, and vice versa. One of the commonest types is that suited for piercing and sucking, that is, for making a hole in the epidermis of a plant or animal and then drinking the sap or blood. In the aphis, which feeds on plant juices, the labium is rolled to form an incomplete tube, in the hollow of which are two pairs of stylets, which are the mandibles and maxillæ (Fig. 17.11). The two maxillæ fit together in such a way as to make two tubes, the smaller of which is used for conveying saliva into the wound, and the larger for taking the food into the mouth. The labium supports the stylets while they make a hole, often deep into the plant tissues, in which process they are aided by the solvent action of the saliva. The sucking is done by the pharyngeal muscles. The mouth-parts of the gnats, some of which also feed on plant juices, and others on blood, are more complicated (Fig. 17.12, A and C). The labium again supports the other parts, and the puncture is made, as before, by the mandibles and maxillæ acting as stylets, but the food canal is made by the almost completely rolled-up labrum-epipharynx, and the salivary duct runs down an elongated hypopharynx. The end of the labium is

expanded into a pair of soft lobes, the labella ; the labium and the structures which it contains are collectively known as the proboscis. Outside this is a pair of maxillary palps. Sucking is carried out by the muscles of the pharynx. Mandibles are absent

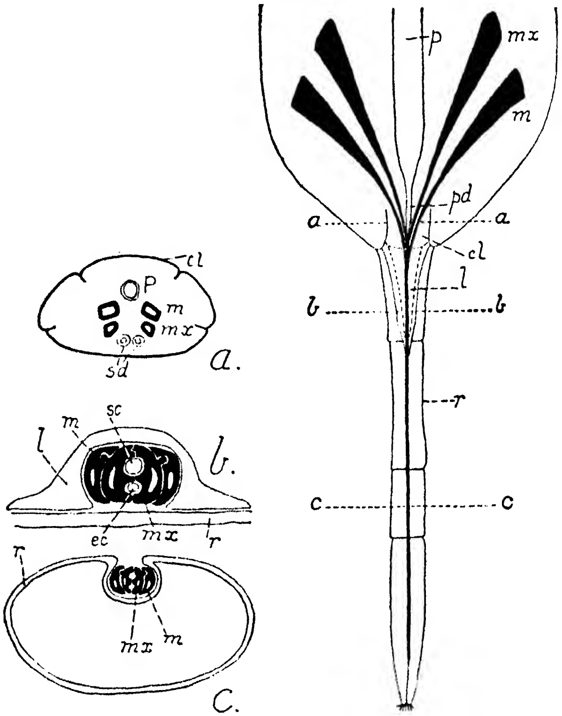


FIG. 17.11.—Diagram of the mouth-parts and adjacent region of the head of a hemipterous insect. On the left are transverse sections (not all to the same scale) at the levels shown by dotted lines of the same lettering.—From Imms, *A General Textbook of Entomology*, 3rd edition, 1934. Methuen, London.

cl, clypeus ; *ec*, ejection canal with salivary duct ; *l*, labrum ; *m*, mandibles ; *mx*, maxilla ; *p*, pharynx ; *pd*, pharyngeal duct ; *r*, labium ; *sc*, suction canal with pharyngeal duct ; *sd*, salivary duct.

from the male, and the maxillæ are represented only by the palps ; he is further distinguished by having longer bristles on the antennæ than has the female. The houseflies and blowflies are incapable of piercing, and can only suck at a surface which is already liquid, or one which can easily be made so. The general pattern of the mouth-parts is similar to that in the gnat, but the mandibles and maxillæ (except the palps) are missing, and the labella are greatly enlarged and covered with grooves called

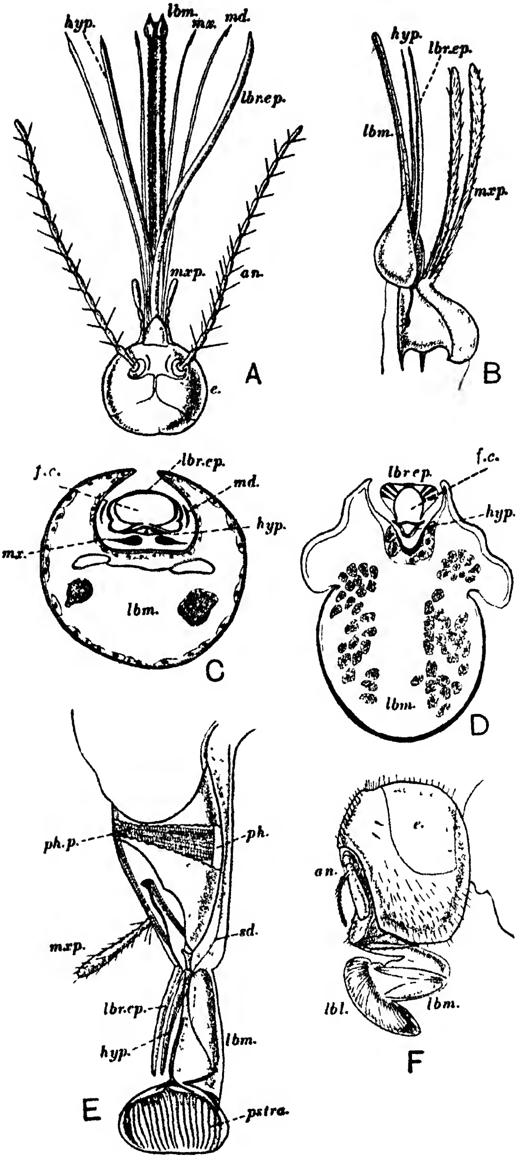


FIG. 17.12 —Mouth-parts of Diptera.—From Borradaile and Potts, *The Invertebrata*, 2nd edition, 1935. Cambridge University Press. A-D after Patton and Cragg.

A, *Culex pipiens* ♀ ; *B*, *Glossina submorsitans* ; *C*, transverse section through proboscis of *Culex* ; *D*, transverse section through proboscis of a muscid fly ; *E*, proboscis of a muscid fly, extended , *F*, the same, half folded.

an., antenna ; *e.*, eye ; *f.c.*, food channel ; *hyp.*, hypopharynx ; *lbm.*, labium ; *lbl.*, labellum ; *lbr.ep.*, labrum epipharynx ; *md.*, mandible ; *mx.*, maxilla , *mxp.*, maxillary palp ; *ph.*, pharynx ; *ph.p.*, pharyngeal pump ; *pstra.*, pseudotracheæ ; *sd.*, salivary duct.

pseudotracheæ, which act like a sponge (Fig. 17.12 F). Solid food is liquefied by the regurgitation of fluid from the gut, and small teeth on the labella can scrape the surface to assist the enzyme action. The butterflies and moths also have mouth-parts suitable for drinking only, their food being the nectar from flowers. The proboscis

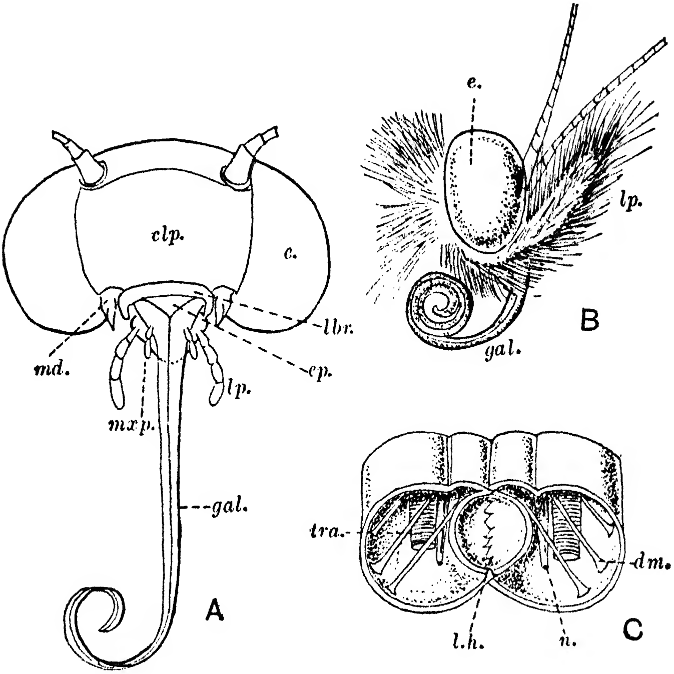


FIG. 17.13.—Head and proboscis of a moth.—From Borradaile and Potts, *The Invertebrata*, 2nd edition, 1935. Cambridge University Press. A and B after Metcalf and Flint, C after Eltringham.

A, Front view ; *B*, side view ; *C*, transverse section of proboscis.

clp., clypeus ; *dm.*, diagonal muscles ; *e.*, eye ; *ep.*, epipharynx ; *gal.*, galea ; *lbr.*, labrum ; *l.h.*, locking hooks ; *lp.*, labial palp ; *md.*, mandible ; *mxp.*, maxillary palp ; *n.*, nerve ; *tra.*, trachea.

is formed of the interlocked galeæ of the maxillæ, and is carried at rest coiled up under the head. All the other parts are reduced or absent except for a three-joined labial palp (Fig. 17.13).

The bees have peculiar mouth-parts best known as licking and sucking (Fig. 17.14) ; they collect pollen as well as feeding on nectar, and also use their mouth-parts for building. The proboscis is formed by the elongated and fused glossæ of the labium, and food is sucked up a groove on the dorsal surface of this. The

well developed labial palp and galeæ surround the glossa and probably help to form the tube. The mandibles are used for building.

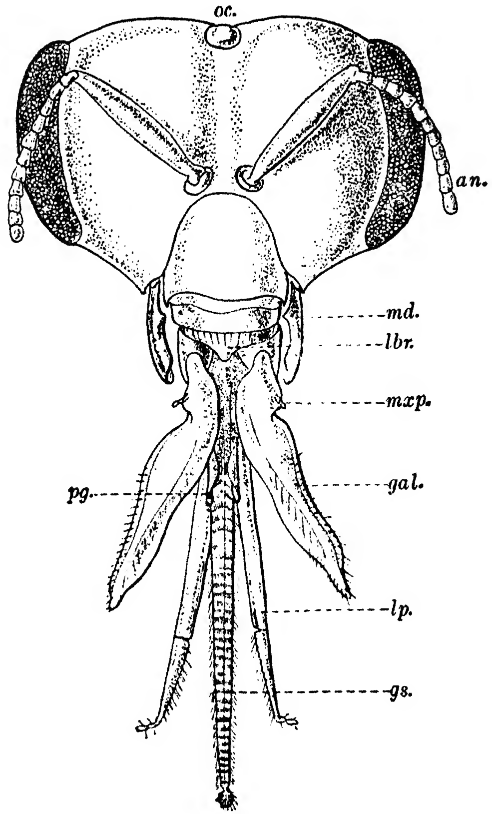


FIG. 17.14.—Head and mouth-parts of a honey bee.—From Borradaile and Potts, *The Invertebrata*, 2nd edition, 1935. Cambridge University Press. After Cheshire.
an., antenna; *gal.*, galea; *gs.*, glossa; *lbr.*, labrum; *lp.*, labial palp; *md.*, mandible; *mxp.*, maxillary palp; *oc.*, ocellus; *pg.*, paraglossa.

WINGS

Although insects are typically flying creatures, wings are absent from the most primitive living orders, and have also been lost by a number of other groups, particularly parasites such as fleas, lice, and bed bugs, but also by some free-living forms. The simplest condition is for both pairs of wings to be functional, membranous, and alike. When both pairs are used they are often locked together, so that they beat as one; the bees have a series of hooks, and the butterflies have interlocking bristles.

The beetles have the front pair of wings modified, even more strongly than in the cockroach, to form hard wing-cases, known as elytra or shards. In the butterflies and moths both pairs are covered with small scales, which also clothe the rest of the body, and come off as a powder when the insect is handled. The flies in the strict sense (Diptera, p. 255) have lost the hind pair, which are represented only by small knobs, the halteres (sing., halter) or balancers, which assist in maintaining the animal's balance in flight.

LIFE-HISTORIES

The different orders of insects have various types of life-history, according to their habitat and evolutionary level, but it is very common for there to be a larva, by which should be meant an immature form, living a life independent of the parents, and possessing structures which are not present in the adult. Since insects are arthropods they undergo the characteristic moults or ecdyses which are necessary to allow the inelastic cuticle to be replaced. The period between two ecdyses is a stadium, and the form of a larva in a particular stadium is an instar. The last instar, which comes after the last ecdysis, is the adult or imago (pl., imagines). The change of a larva to an adult is metamorphosis. The insects may be divided into a number of groups according to their life-histories ; these groups correspond only partially to the subclasses of the formal classification.

The Ametabola are those which have no larva and no metamorphosis ; the form hatched from the egg is not mature, but differs from the adult in hardly anything but the reproductive system, which gradually develops. This group includes the primitive wingless insects such as silverfish and springtails, and a number of wingless members of other groups, such as the lice and the workers of termites.

In the Paurometabola the young instars differ from the adults not only in having undeveloped gonads but in not possessing wings ; they have, however, no positive characters of their own, and are not strictly larvæ although often called so. They are known as nymphs, which, since the word means, in origin, maidens fit for marriage, is a somewhat inappropriate term for sexually immature animals. Development consists in the growth of the reproductive organs, and in the gradual formation of wings. In this group comes the cockroach, and most of the orders of insects which in the formal classification are called

Exopterygota. There is no metamorphosis, although entomologists often speak as if there were.

The Hemimetabola are similar to the Paurometabola, but differ in that the young stages live in water and have peculiar features, suited to the habitat, which are absent from the adult; they are, therefore, true larvæ. They are often called nymphs, but a better term is naiads, which points out both their similarity to and difference from the nymphs of the Paurometabola. (In Greek mythology the naiades were water-nymphs.) There is necessarily a metamorphosis, which takes place as the animal emerges from the water. In the mayflies, for instance, the naiad crawls up a plant stem into the air, and goes through an ecdysis which produces a winged instar. After a short time a final moult produces the imago. There is here foreshadowed the connection of metamorphosis with moulting so notable in the higher insects. The Hemimetabola include only the stoneflies, dragonflies, and mayflies. The sole larval characters of the first are the gills, but the naiads of the last two possess also mouth-parts different from those of the adult.

The Paurometabola and Hemimetabola are usually grouped together as Heterometabola, an assemblage of orders almost equivalent to the subclass Exopterygota, but this connection obscures the important formal difference between nymph and naiad.

The remaining insects are Holometabola. There is a true larva in every sense of the word, and so a true metamorphosis. The features in which the larva differs from the adult are its general form; the immaturity of its gonads; the presence of internal wing buds instead of wings; the mouth-parts; and the possession of small lateral simple eyes or ocelli in place of compound eyes. In addition aquatic larvæ possess respiratory adaptations. The Holometabola comprise all the typical members of the subclass Endopterygota. There are several different types of larvæ, such as those which, possessing only thoracic legs, resemble the primitive wingless insects and are called oligopod or campodeiform (e.g. the water-beetle *Dytiscus* and other beetles), the caterpillars of butterflies and others, which have abdominal legs as well as thoracic, and are called polypod or eruciform, and the apodous or limbless grubs or maggots of flies. In several insects more than one type of larva is found in a single life-history, when hypermetamorphosis is said to occur.

Metamorphosis is concentrated into a restricted stage of the

life-history, that of the penultimate instar, which is called a pupa. In most Holometabola the wings and legs have no secondary attachment to the body and may be capable of some movement; the pupa has a form roughly between that of the larva and the adult, and is called exarate. In butterflies and moths, some beetles, and most two-winged flies, the limbs, though just visible externally, are closely glued down to the body by the moulting fluid of the previous ecdysis, such a condition being called obtect. In the houseflies and their relatives the pupa is coarctate, that is, enclosed in the last larval skin, called the puparium, and no limbs are visible. The typical pupa is inactive, quiescent, and incapable of feeding. Inside its skin a great deal of breakdown of the body goes on, largely by phagocytosis (p. 190), and the form of the imago is built up by the division and growth of persistent embryonic cell masses called imaginal discs. The gut, limbs, many muscles and many tracheæ are often completely replaced in this way. The nervous system persists throughout metamorphosis, although there may be much growth and alteration, especially of the brain; the heart beats throughout pupation and undergoes only slight changes. The gonads grow throughout life, and in a few species even become functional in the larva. Finally the pupal skin splits and the imago emerges. Pupation, like ecdysis, seems to be generally under the control of hormones. An imaginal hormone, secreted in a part of the brain called the pars intercerebralis, activates the thoracic gland (cells of the fat-body of the pro- and meso-thorax) to produce another hormone which stimulates epidermal cell-division and the secretion of a new cuticle; it therefore induces moulting. In most insects the thoracic glands atrophy in the adult and so moulting does not continue. A third hormone, sometimes called the juvenility factor, is secreted in the corpora allata, a part of the nervous system near the heart. It stimulates the growth of the nymph, but suppresses imaginal characters; metamorphosis can only occur when production of the juvenility factor is reduced. Whether this is gradual, or in two well-marked stages, determines the absence or presence of a pupa.

The instar before the pupa is often slightly specialised, and is known as the prepupa. The rudiments of the limbs and wings, which in the larva are held in sacs of the body-wall, become everted, and the animal's behaviour changes. It is the prepupa of butterflies which seeks shelter and spins the cocoon or mat.

CLASSIFICATION

The classification of insects is based primarily on the presence or absence of wings, on the way in which these develop, and on the degree of metamorphosis. Some of the wingless insects, however, resemble so closely those which possess wings that they are generally considered to have lost wings which their ancestors once possessed, and are grouped with the winged orders. It is for this reason that the names of the groups, derived from the condition of the wings, are sometimes unfortunate ; by no means all wingless insects are Apterygota, although that word means ' creatures without wings '. It is very common now to use the terms descriptive of the type of metamorphosis (Ametabola, etc.) as alternative taxonomic proper names to those ending in -pterygota, which refer to the wings. This introduces a second set of illogicalities, and it is simplest to use the terms ending in -metabola only as descriptions of the actual degree of metamorphosis undergone.

CLASS I—APTERYGOTA

These are primitively wingless and the abdomen bears appendages of various sorts in addition to the external genitalia and cerci. There are four orders : (1) the DIPLURA, (2) the THYSANURA or bristle tails, (3) the COLLEMBOLA or springtails, and (4) the PROTURA. The first, second, and third have biting mouth-parts, the fourth piercing. The commonest example is the silverfish, *Lepisma saccharina*, a thysanuran, which is a frequent inhabitant of cupboards, bookcases and cracks in the floorboards of houses, and the largest is the shore-living *Petrobius maritimus* (Fig. 17.15), also a thysanuran.

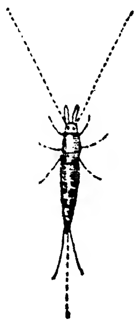


FIG. 17.15.—*Petrobius maritimus* × 1.—From Sandars, *An Insect Book for the Pocket*, 1946.

CLASS II—PTERYGOTA

These are insects which possess wings, or, if they do not, closely resemble in other respects species which do. They are divided in some recent classifications not into the two subclasses given below but into four divisions on the basis of their ancestry and the arrangement of various internal organs.

SUB-CLASS I—EXOPTERYGOTA

The wings develop outside the body. There are several orders mostly with biting mouth-parts. There is no larva in the strict sense except in those orders which have aquatic naiads.

Order 5. EPHEMEROPTERA. The most striking feature of the mayflies, and that which gives its name to the order, is the brief life-span of the imago, sometimes a mere day, and never more than a few. The imagines do not feed, and have vestigial mouth-parts, but those of the larvæ are biting. The larvæ are aquatic naiads, which, except in the first instar, possess tracheal gills, like small wings, attached to the abdominal segments (Fig. 17.16). Both imago and larva have long cerci and a long caudal filament, giving a characteristic triple tail which makes them easy to recognise.

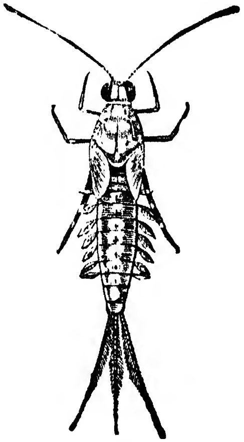


FIG. 17.16.—Mayfly larva. From Thomson, after Eaton.

Showing tracheal gills, and wings appearing in front of them.

Order 6. ODONATA. The dragonflies are large insects with biting mouth-parts, predacious in both larval and adult stages ; the eyes are big and the antennæ reduced. The larvæ are naiads with tracheal gills either at the posterior end of the body or in the rectum, and a characteristically modified labium known as the mask ; this is normally carried folded under the head, but can be suddenly shot out to seize an animal such as a tadpole.

Order 7. PLECOPTERA. The stoneflies have biting mouth-parts and aquatic larvæ (naiads) with tracheal gills—expansions of the body-wall richly supplied with tracheæ. *Perla carlukiana* (=*marginata*) is common by English streams.

Order 8. GRYLLOBLATTODEA, a small order of wingless insects, includes a few species only, including the genus *Grylloblatta*, which is possibly near the base of the ancestral line of the exopterygota.

Order 9. ORTHOPTERA. This includes the locusts, crickets, grasshoppers and in many ways, such as biting mouth-parts and hardened forewing, they resemble the cockroach, but the hind legs are elongated for jumping. Many of them are notable for the

way in which they chirp or sing by rubbing wings or legs against some part of the body, and for the presence of ears by which the noise made by another individual is heard. The song is largely sexual in character.

Order 10. PHASMIDA. The stick and leaf insects are relatively large, with bodies elongated and either cylindrical or depressed, so that they resemble pieces of vegetation. The mouth-parts are mandibulate.

Order 11. DERMAPTERA. These are the earwigs, which closely resemble the Orthoptera but are always recognisable by the

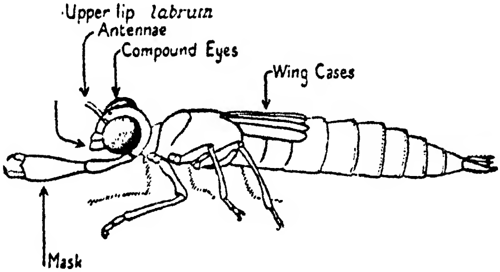


FIG. 17.17.—Dragonfly larva.—From Sandars, *An Insect Book for the Pocket*, 1946.

gripping forceps, which is a modified pair of anal cerci, at the posterior end of the body. The mouth-parts are biting. The common earwig is *Forficula auricularia*.

Order 12. EMBIOPTERA, has many apterous forms.

Order 13. DICTYOPTERA includes the mantids and cockroaches, the character of which have been seen in the previous chapter.

Order 14. ISOPTERA. The termites or white ants, commonest in the tropics, are remarkable for their social organisation, which closely parallels that of the true ants, to which they are not nearly related. Most of the individuals are sterile and wingless workers and soldiers of both sexes. Each colony is founded by a royal pair, the king and queen, which at first have wings, but they lose these when they settle down in matrimony. Many termites feed solely on wood, but they can only do so with the help of symbiotic flagellate Protozoa which inhabit the gut and break down the lignin. Experimentally termites can live on the purest cellulose known, and the source from which their symbionts obtain nitrogen remains a mystery. The mouth-parts are biting.

Orders 15, ZORAPTERA, and 16, PSOCOPTERA, are small orders of

small insects, with many apterous forms. *Trogium* (=*Atropas*) *pulsatorium*, the book-louse (Psocoptera) is notorious for living on the paste of book-bindings, but it is not confined to this diet.

Order 17. MALLOPHAGA. The bird lice are wingless and have biting mouth-parts with which they feed on particles of feather or (for some are parasitic on mammals, not birds) hair. The chief zoological interest of the Mallophaga lies in the attempt which has been made to use them in avian taxonomy. Since the families of

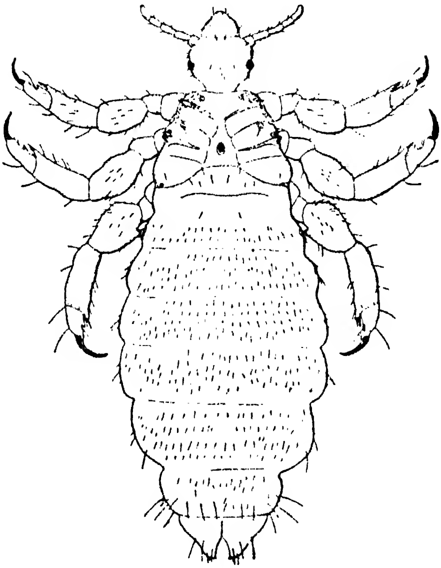


FIG. 17.18.—The body louse in dorsal view × *c.* 50. After Nuttall.

lice are in general restricted to particular groups of birds, it has been suggested that when the affinities of the lice are clearer than those of the birds, the classification of the birds may be based on that of the lice.

Order 18. SIPHUNCULATA OR ANOPLEURA. The sucking lice, or simply lice, are wingless ectoparasites of mammals and have piercing mouth-parts. Two species are found on man, *Pediculus humanus* (Fig. 17.18) and *Phthirus pubis* (Fig. 17.19). The latter, the crab or pubic louse, is found chiefly, though not solely, on the hairs of the pubic region, and is of no great medical importance. *P. humanus* occurs in two forms, the body louse, *P. humanus corporis*, found only on the body and its clothing, and the head louse, *P. humanus capitis*, found on the head and occasionally

elsewhere. These were formerly considered to be different species. Both transmit the parasites which cause typhus, trench fever, and relapsing fever, the first two being organisms of doubtful nature called *Rickettsia*, and the third the bacterium *Treponema* (=*Spirochæta*) *recurrentis*. Lice are common in almost all crowded aggregations of man, whether they be primitive tribes, urban schools, or prisons. Anything which leaves the lice to a peaceful life, such as unchanged clothes, or long hair (and especially permanent waves), will encourage them, but the individual infestation is seldom more than twenty. Since neither

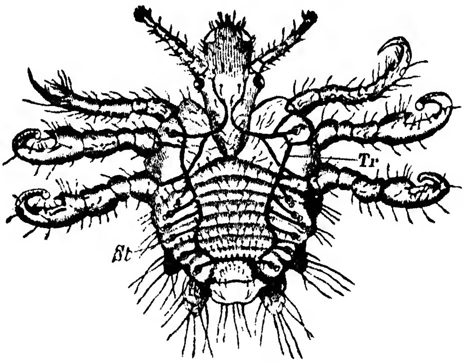


FIG. 17.19. The crab louse (*Phthirus pubis*).—From Sedgwick, after Landois. *St.*, Stigma; *Tr.*, trachea.

the insects nor their eggs can live long away from man, the chief method by which the parasites spread is personal contact. Infection may, however, take place through towels or combs or stray hairs, especially when these bear the eggs or nits, and since the lice can move at about nine inches per minute, propinquity to an infected person is almost as dangerous as contact. Lice may be completely removed from the body and hair by disinfectants, and from clothes by very moderate temperatures (53·5° C. for five minutes kills both insects and eggs). Persons who wash, and change their clothes with some frequency, are never likely to become more than temporarily and lightly infected.

Order 19. HEMIPTERA or RHYNCHOTA. These are generally known as bugs, although they include many species, such as the water scorpion (*Nepa*) and water boatman (*Notonecta*), to which the term is seldom applied. All have piercing and sucking mouth-parts of the same general type as those of the aphis, which has been

described above (p. 239), but while most feed on plant juices, some, such as the bed-bugs (*Cimex*, Fig. 17.20) suck blood. Many of the herbivorous forms are of great economic importance both because of the direct damage which they do and because of the virus diseases which they carry. Many species, such as the bed-bugs, are wingless, while others, such as the Aphididæ or greenflies (Fig. 17.21) have wingless forms. This last family is also of interest for its peculiar and complicated life-cycles, which are generally of the following pattern. An egg which has survived the winter hatches in spring to form a wingless female. She feeds, and rapidly produces about forty young ones ; these are all wingless females, have been formed by parthenogenesis, that is, from eggs which have not been fertilised, and are hatched within the body of their mother, so that they are said to be produced viviparously. Each in its turn reproduces in the same way, and similar generations occur throughout the summer. There is thus

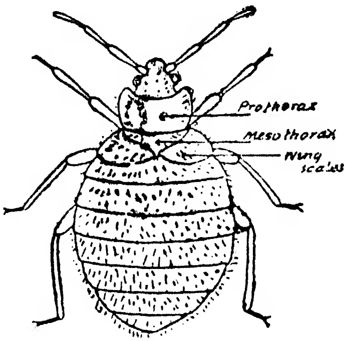


FIG. 17.20.—The bed-bug, *Acanthia* (=*Cimex*) *lectularia* × c. 12.—From Murray, after Butler.

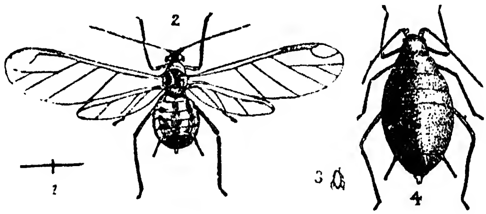


FIG. 17.21.—The turnip-leaf planthouse (*Aphis rapæ*).—After Curtis. 2 and 4 winged and wingless parthenogenetic females 1 and 3 natural size of the same.

very rapid multiplication but little spread of the animal. Eventually, in late summer, a winged brood appears, and some of the bugs in this are males. The winged forms fly to neighbouring plants and copulate. Each female then lays one fertilised egg, which may survive the winter and start a new cycle in the spring. There are variations on this theme, mostly in the direction of greater complexity. *Doralis* (=*Aphis*) *rumicis* lays the fertilised eggs on the spindle tree, *Euonymus europaea* ; after a few wingless

generations have been produced in the early summer, winged, but still parthenogenetic, females appear, and migrate to beans (*Vicia*) and other plants, where more parthenogenetic broods, some winged and some wingless, are produced. When the winged sexual individuals are formed, both sexes migrate back to the spindle tree.

Order 20. THYSANOPTERA. These are the thrips, small insects with sucking mouth-parts, mostly feeding on plants, of some economic importance.

SUB-CLASS II—ENDOPTERYGOTA

The wings develop in sacs which are pushed inward from the surface of the body. There is a true larva, and at metamorphosis, which is restricted in time, the wings are everted. Some orders have biting mouth-parts, but the majority have specialised mouth-parts of various kinds.

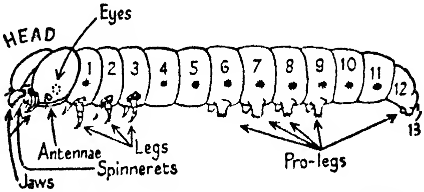
Order 21. NEUROPTERA. This is the rump of a much larger Linnæan order, and as now defined it includes insects with biting mouth-parts and a characteristic ladder-like venation on the fore edge of the wings. The alderfly, *Sialis lutaria*, has an aquatic larva with long tracheal gills, and biting mouth-parts, and the lacewings, *Chrysopa*, have terrestrial larvæ with peculiar sucking mouth-parts. All neuropteran larvæ are carnivorous and campodeiform (p. 245).

Order 22. MECOPTERA. This is a small order with biting mouth-parts, eruciform larvæ (p. 245) and external male genitalia which superficially resemble the tail of a scorpion. An example is *Panorpa communis*, the scorpion fly.

Order 23. TRICHOPTERA. The caddis flies are well known for their aquatic caterpillars which build themselves cases of sticks or stones from which only the head and thorax protrude. The mouth-parts of the larvæ are biting, but in the adults the mandibles are vestigial, and if they eat anything it can only be liquid. The bodies are covered with hair-like processes. The larvæ have tracheal gills.

Order 24. LEPIDOPTERA. The butterflies and moths have larvæ which are caterpillars and have biting mouth-parts, and adults with characteristic sucking mouth-parts which have been described on page 242. The body and wings are covered with scales. The pupa is often enclosed in a cocoon spun of silk secreted by the larva through spinnerets on the head. A diagram of a typical

larva is shown in Fig. 17.22. The prolegs, though not fully formed, are relics of true abdominal appendages. The eggs of a butterfly are laid on a food plant which is characteristic of the species ; they hatch into larvæ of the first instar. These begin eating and grow rapidly, and about four ecdyses (the number is constant for the species) take place. The larval instars generally differ slightly in appearance, as well as in size. The last larval instar, or prepupa, becomes nomadic, and goes in search of a place suitable for pupation. It then spins silk, which is used either as a mat, from which the larva hangs itself by the claspers, or a girdle, by which the larva binds itself to a plant stem, or a cocoon like that of the silkworm. Next the larval skin is split and shed, and a new pupal



17.22.—A caterpillar.—From Sandars, *An Insect Book for the Pocket*, 1946.

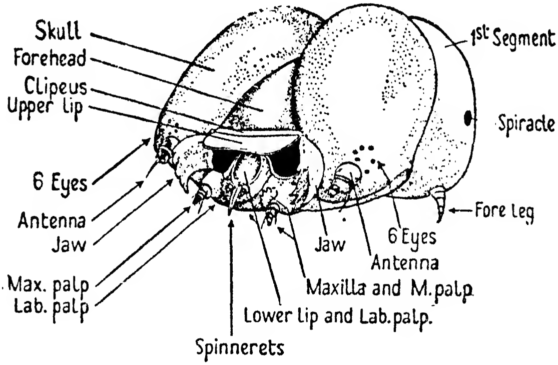


FIG. 17.23.—Head of caterpillar.—From Sandars, *A Butterfly Book for the Pocket*, 1939.

skin is formed which completely encases the body and limbs ; there are no breaks in this skin except for the spiracles. Such a completely encased pupa is called obtect. After an apparent rest, during which metamorphosis has been going on, the pupal skin splits down the middle of the back, and the butterfly crawls out. The wings are at first limp and small. They are steadily expanded, largely by the inflation of their tracheæ with air, until they have about nine times their original area. In the process the wing has

changed from a hollow bag to a flat double membrane. There may be one, two, or three generations in the year, according to the species. The winter is passed in a quiescent state, sometimes as an egg, sometimes as a larva, sometimes as a pupa and sometimes as an adult, but in British species, with one exception, there is only one method of wintering in each. The large white, *Pieris brassicæ*, lays its eggs in batches of six to a hundred on leaves of plants of the family Cruciferæ, such as cabbages and turnips. The black and yellow larvæ hatch in from four to seventeen days, and are gregarious, feeding together on a mat of silk which they have spun over the leaf. There are four moults, and the pupa is formed after about a month. It is fastened to a support both by a girdle of silk round the body and by a terminal pad in which the claspers are embedded. There are two or three generations in a summer, and while the earlier caterpillars may pupate on the food plant, the later ones usually carry out a vertical migration and anchor themselves on the under side of a ledge of a wall or fence. Metamorphosis takes about a fortnight, but the late summer pupæ have their development inhibited by the cold weather, and may survive the winter. If they do, the imago emerges in April. Butterflies of the first generation are on the wing from April until June, and those of the second from June until the end of August. In favourable weather there may be a third generation which flies until October. A few imagines survive the winter, but generally an individual does not live for much over three weeks, and feeds on the nectar of several flowers, especially beans, clover, and lucerne. These are Leguminosæ, a different family from that to which the food plants of the larvæ belong. Examples of butterflies which winter in other ways are the brown and purple hairstreaks, *Thecla betulæ* and *T. quercus* (eggs), the meadow brown, *Maniola jurtina* (larvæ), and the small tortoiseshell, *Aglais urticæ*, and brimstone, *Gonepteryx rhamni* (imagines). It is natural that most of the earliest butterflies of spring should be those which have survived the winter in the adult state.

Order 25. DIPTERA. These are ' flies ' in the narrow sense, two-winged insects with the hind pair replaced by knobbed balancers. The mouth-parts are sucking but may also be piercing, either primarily by means of mandibles, as in the gnat described on page 239, or secondarily by stiffening of the labella, as in the tsetse fly *Glossina* and the stable fly *Stomoxys*. The three thoracic

segments are fused. The larva is apodous (Fig. 17.24), and the pupa may be obtect (though often capable of movement) or coarctate. The gnats or mosquitoes lay their eggs on the surface of water, different species requiring different ecological conditions of size of pond, temperature, hydrogen ion concentration, salinity, and so on. The larvæ, although legless, are very active, and swim beneath the surface by a wriggling movement of the whole body (Fig. 17.25) ; they feed on minute particles in the water by means

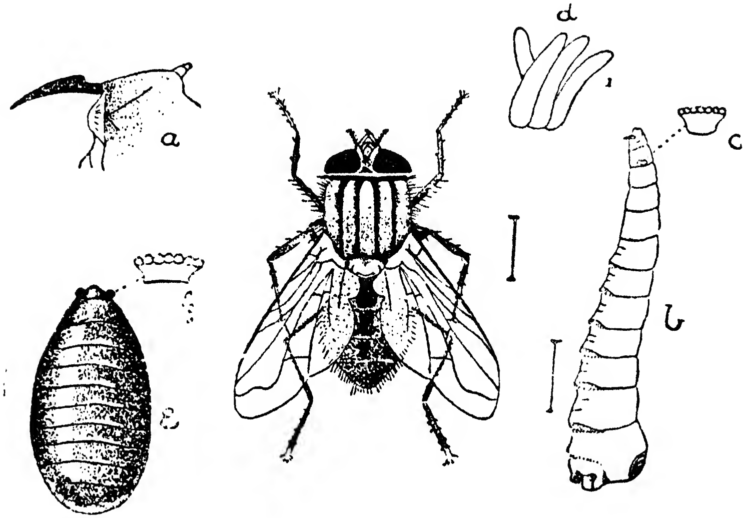


FIG. 17.24.—The life-history of the housefly (*Musca domestica*).—From Theobald. *a*, Mandible of larva with adjacent structures ; *b*, larva ; *c*, anterior spiracle of the same ; *d*, eggs ; *e*, pupa case ; *f*, remnants of spiracle on the same.

of brush-like structures which continually sweep a current of water into the mouth and are combed by the mandibles and maxillæ (Fig. 17.26), and breathe air which they obtain at the surface. Most of the spiracles are closed, but the two main tracheal tubes open on a projection of the eighth segment of the abdomen called the respiratory siphon. This is closed with flaps when the creature is under the water, and when it comes to the surface they spread out on the surface film, expose the tracheal openings to the air, and hang the insect from the film. Water, which has high surface tension, will not enter the narrow tube, but oil, with low surface tension, will, as can easily be observed under the microscope ; this is the principle of the method of attacking the carriers of malaria (p. 68) by spraying paraffin on the water. After four

months the larva becomes a pupa, which is shaped like a comma. It can swim, in much the same way as the larva, but instead of having one respiratory siphon on the abdomen it has two just behind the head, which are used in the same way. The pupa does not feed, and after a few days the adult gnat emerges into the

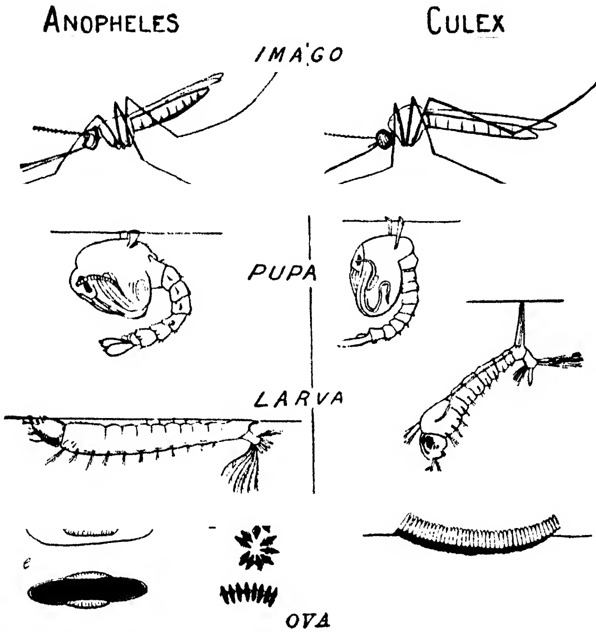


FIG. 17.25.—A comparison of the various stages in the life-history of Anopheles (left) with those of Culex (right).—From Shipley.

Note how the larvæ and pupæ hang from the surface film of the water (represented by a thin line). The organs by which they are suspended contain air tubes, and if these be prevented by a film of paraffin from functioning the insect is drowned. Note also that the eggs of *Culex* cling together as a raft. *e*., two views of an egg, magnified.

air through a dorsal split, standing on the floating pupal skin until its own has hardened. There are several generations in the course of the year.

The mouth-parts of the housefly (*Musca domestica*) have been described on page 240. The eggs are laidin any rotting organic matter, particularly stable manure, and hatch, in eight to seventy-two hours according to the weather, into maggots or gentles. These are soft, white and legless, and shaped like an ice-cream cone. There are twelve segments, and the head at the pointed end can be withdrawn under the first segment and carries

a pair of hook-like mandibles and a pair of minute antennæ. The mandibles help to draw the animal forward; it moves

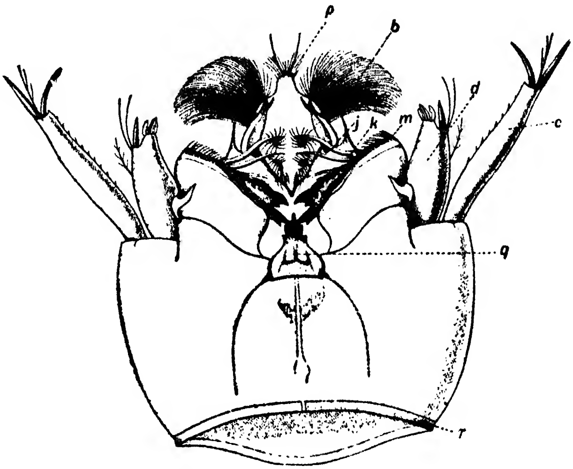


FIG. 17.26.—A ventral view of the head of a fully grown larva of the gnat *Anopheles maculipennis*.—From Nuttall and Shipley.

b., Brush with which food is swept from the surface film of the water (*Culex* larvæ, hanging with the head down, collect from a lower stratum); *c.*, antenna; *d.*, palp of maxilla; *j.*, stout hairs which arrange the brush; *k.*, teeth of mandible; *m.*, hooked hairs at edge of maxilla; *p.*, a median tuft of hairs; *q.*, a median structure known as the metastoma; *r.*, rim of head.

rapidly away from light so that it tends to burrow into organic matter, on which it feeds. Food is liquefied by a salivary secretion

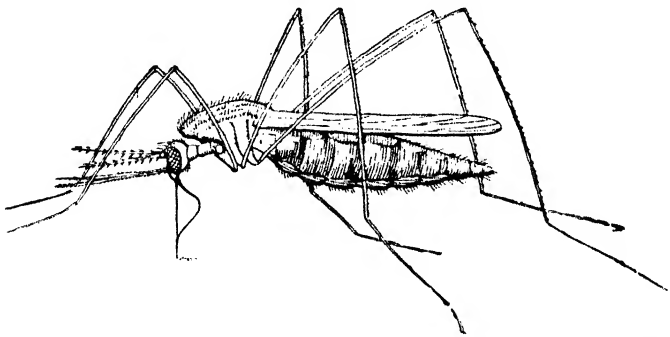


FIG. 17.27.—A gnat, *Anopheles*, sucking blood.—After Nuttall and Shipley.
The curved line under the head is the labium.

and then sucked in. The second and last segments bear a pair of spiracles each, and the fifth and following somites have each a spiny pad below. The last larval instar buries itself, often away

from its food, to a depth of an inch or so, and pupates, the pupa being enclosed in the last larval skin. The imago, which flies towards light, i.e. is positively phototactic, escapes by the inflation of a peculiar bladder or ptilinum on its head. This is filled with blood under pressure, and used to break successively the pupal skin and puparium, and then to make a way to the open air. The length of life of the larva is from two days to eight weeks, and of the pupa from three days to four weeks or more, according to the temperature, and the imagines may be capable of laying eggs a fortnight after emergence ; a complete generation may therefore be accomplished in three weeks. The first house-flies of the season appear in Great Britain in June and, except for a few which linger indoors, the last are seen on the wing in October or November. Where flies go in the winter time is still unknown. A few may remain as dormant larvæ, pupæ or imagines, but it is also possible that all die and that those which appear the next summer are immigrants from warmer countries where breeding continues throughout the year. Many imagines are killed at the onset of winter by a fungus, *Empusa muscæ*, which continues to live saprophytically after the fly has died, and may surround its corpse with a grey halo of hyphæ. Other related species hibernate as adults.

The blowflies or bluebottles (*Calliphora*) lay their eggs on flesh and have a similar life-history to the housefly. Other Diptera are the warble flies and bot flies (Oestridæ) with larvæ parasitic on hoofed mammals, the hover flies (Syrphidæ) which superficially resemble bees, the gadflies or clegs (Tabanidæ), midges (Chironomidæ), and daddy-long-legs or crane flies (Tipulidæ), the larvæ of which are leather-jackets.

The above five orders of the Endopterygota are sometimes regarded as being much more closely related to each other than are the remaining three ; they may have been derived from a common ancestor which was not unlike a member of the Mecoptera.

Order 26. SIPHONAPTERA OR APHANIPTERA. The fleas, such as *Pulex irritans*, the human flea (Fig. 17.28), are ectoparasites of mammals and have piercing and sucking mouth-parts. There are no wings, and the body is strongly laterally compressed. The adults, which alone suck blood, can live for a short time away from their host, and leave him to lay their eggs. The larvæ have biting mouth-parts, and feed on organic matter in dust. *Pulex*

irritans pupates in a cocoon after a larval life of about twelve days. The rat flea, *Xenopsylla cheopis*, which occasionally sucks the blood of man, carries the germ which causes bubonic plague.

Order 27. COLEOPTERA. The beetles (Fig. 17.29) are a very large order of insects of a characteristic form, easily recognised by the straight longitudinal line made by the meeting of the wing cases. The mouth-parts are biting, and the fore wings are modified as hard elytra. The larvæ are of various types, and hypermetamorphosis sometimes occurs.

Order 28. STREPSIPTERA. These insects are small, with degenerate biting mouth-parts, and are perhaps derived from the beetles.

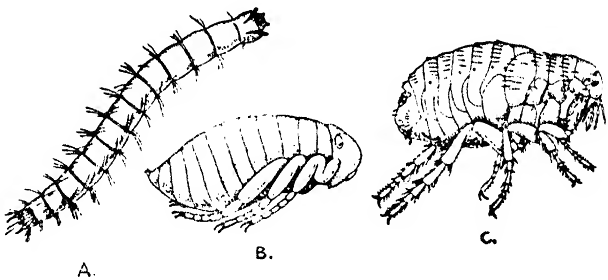


FIG. 17.28.—The common flea (*Pulex irritans*) × *c.* 12.
A, Larva ; *B*, pupa ; *C*, adult.

The larvæ and usually the adult females are endoparasites of other insects, and the males have the fore wings reduced to knobs.

Order 29. HYMENOPTERA. This is an important order, including ants, sawflies, wasps, and bees. The mouth-parts are primarily biting, but may secondarily be developed for sucking, as in the honey bee described on page 242. The hind wings are smaller than the fore wings, to which they are attached by hooks. There is usually a distinct waist, which is between the first and second abdominal segments, the former being fused to the metathorax. The abdominal appendages include an ovipositor, which may be modified as an instrument for stinging or boring. The larvæ are either legless or caterpillar-like, and the pupa is exarate. Some families, such as the Ichneumonidæ, have larvæ which are endoparasites of other insects.

The most striking thing about the Hymenoptera is the social organisation, which has been developed in several groups, and which is paralleled elsewhere only in the termites (p. 249). Many

bees are solitary, but the hive or honey bee, *Apis mellifica*, has one of the most elaborate social organisations in the order. It is impossible to describe the life-history in the usual way, for new colonies start, not with one individual, but with a large group, and we must therefore begin by considering the structure of an established community. This will consist of a fertile female or queen, bearing in her spermatheca a supply of sperms, a number of males or drones, and many thousands of sterile females or workers. The chief external differences between these three castes are shown in Fig. 17.30. The drones have no stings. The workers have structures on the third legs called pollen baskets, and their

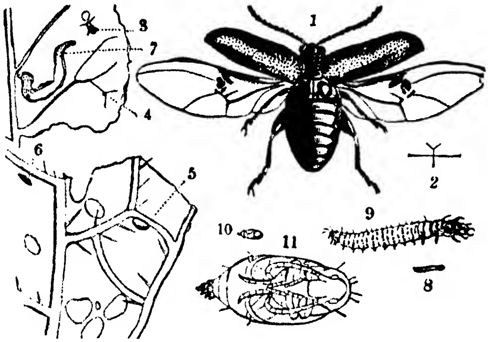


FIG. 17.29.—The turnip flea beetle (*Haltica nemorum*).—From Theobald.

1, Adult, magnified; 2, true length and wing expanse; 3, adult feeding on leaf; 4, egg, natural size; 5, the same magnified; 6, 7, tunnel made by larva in leaf; 8, 9, larva, natural size and magnified; 10, 11, natural size and magnified view of pupa, which lies in soil.

This very destructive insect feeds, as larva and adult, on the leaves of turnips, cabbages, broccoli, and other Cruciferæ. It has many broods in the year, the last hibernating under stones, etc. Its worst damage is done to seedlings. Paraffin, derris powder, and a mixture of soot and lime are remedies.

stings are powerful and poisonous. The workers spend the day, or at least the shining hours, gathering pollen as well as honey, or, more strictly, nectar, from every suitable flower. When they return to the hive they regurgitate the nectar as honey, and store both this and pollen in special compartments or cells. They also build the combs and carry out various chores. The hexagonal cells are made of wax which comes from between the abdominal segments, and is chewed and placed in position by the jaws. The cells are of regular shape, hexagonal in cross-section, but not all of the same size. The larvæ and queen are fed, dead bodies removed, and the younger workers fan with their wings to ventilate and cool the hive.

The fecundated queen lays eggs, placing each carefully in a

cell. Not all the eggs are fertilised ; if a sperm is released in the act of laying, syngamy follows and the larva produced is female ; if no sperm is released, the resulting parthenogenetic larva will become a drone. The drone eggs are also placed in larger cells than those of the workers. All larvæ are fed by the workers, at first on 'royal jelly', which is secreted by their pharyngeal glands. Drone and worker larvæ are changed to a diet of honey and predigested pollen on the fourth day. A few female larvæ, which come from eggs which have been laid in larger cells, are kept on royal jelly throughout ; they develop into queens. Such big cells are made only after the colony has been growing for some time, and there are normally only a few of them. Before any of the new queens emerge the old queen will have left the hive, attended by about half the workers, the whole mass forming

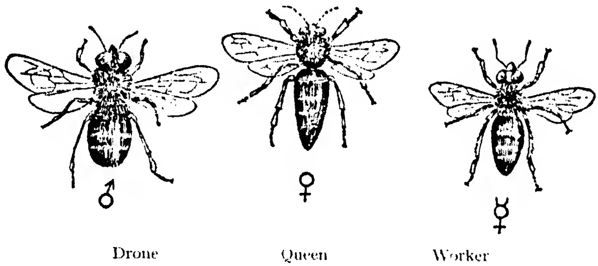


FIG. 17.30.—The honey bee.—From Sandars, *An Insect Book for the Pocket*, 1946.

a swarm which will settle and start a new colony. The first of the new queens to emerge stings the other pupal queens to death, and then, after short flights to learn the neighbourhood of the hive, she soars towards the sun in a nuptial flight, followed by all the drones in the district. The first to reach her copulates in the air. All his sperms are passed into the queen, and in separating from her he is so damaged that he dies. The other drones return to the hive, but will after a time be killed or denied admittance by the workers. The queen also returns, and from then on, until it is her turn to swarm, does nothing but go from cell to cell laying eggs. Her total life may be three or four years.

It is probable that the workers go through a regular series of duties in their life of less than two months, at first fanning the hive and feeding the larvæ, then building, and relieving other workers of their honey and pollen, and lastly, going foraging. It has recently been shown that when a foraging bee returns it

may perform a dance, which indicates to the other bees the direction (relative to the sun) and distance away of the flowers from which they have obtained the food.

The social life of the ants, such as *Formica rufa*, the wood ant, which builds large nests of pine needles or twigs, differs in many respects from that of the bees. A nuptial flight occurs, but many queens and males go together; the female in copulation gets a supply of sperms for life, and the male thereafter dies. The queen sheds her wings by rubbing them off; she may return to her own nest, or go to another of the same species, where she joins the existing community, or she may make a hole in the ground, lay eggs, and wait for them to hatch. She feeds them by regurgitation of material obtained from her own stores of fat, and in due course they become sterile female workers. They build the nest, fetch food, and establish a new colony in which the queen does nothing but lay eggs, which she does every ten minutes for some six years. The general duties in the nest—feeding the larvæ and queens, building, and so on—parallel those of the worker bees, but differ in detail. The food is largely, but not entirely, vegetable matter, and many ants are fond of the liquid which exudes from the anus of aphides. Because of the acquisition of new queens the life of the community is indefinite. A new community is sometimes founded by a group of members of an old colony marching out to build a new nest. The workers of many species of ant, including *Formica rufa*, are of more than one type; morphological differences correspond to differences in duties. It is probable, but not proven, that, as in the honey bee, the cause which determines whether a female egg shall become a worker or a queen is the nutrition which it receives.

18

MOLLUSCS

SNAILS

SEVERAL species of snail are found in Britain, some living amongst land vegetation and others in fresh water. The two most frequently studied are the garden snail, *Helix aspersa*, and the larger Roman or edible snail, *H. pomatia*. The following description applies, except for certain points, to both. *H. aspersa* is widespread in thick vegetation, although it is rare in or absent from many districts in which the soil is deficient in lime ; *H. pomatia* is much more local in its distribution, and although it was previously thought to have been introduced by the Romans, who are known to have cultivated it for food, its shells have now been found in pre-Roman deposits. Both species are in fact edible, and eaten ; *aspersa* was especially sought after in the glass-blowing districts, where it was considered good for the wind, while *pomatia* is the *escargot* of French menus.

When a snail is moving (Fig. 18.1) there are three obvious divisions of the body ; an anterior head, not sharply marked off, but bearing the mouth and two pairs of tentacles, of which the posterior pair are longer and bear eyes ; a long muscular foot, on which the animal moves ; and the dorsal shell, inside which is the visceral mass or hump. Below the edge of the shell is a thick, fleshy rim called the collar ; this is the edge of the mantle, which is referred to below. A number of openings can be seen. Below the shell on the right side is a conspicuous pulmonary aperture, which opens not into the body but into a space called the mantle cavity, within the shell. Just inside the pulmonary aperture is the opening of the excretory duct, and just behind this is the anus. On the right side of the front part of the foot a groove runs forward to the common genital aperture just behind the second tentacle. The foot consists of longitudinal muscle fibres, and if a snail be watched crawling on a glass plate, waves of contraction can be seen running from tail to head along its length. The contact between the foot and the surface on which it moves is lubricated by mucus discharged by a pedal gland which opens just below the mouth. The snail occasionally moves by raising

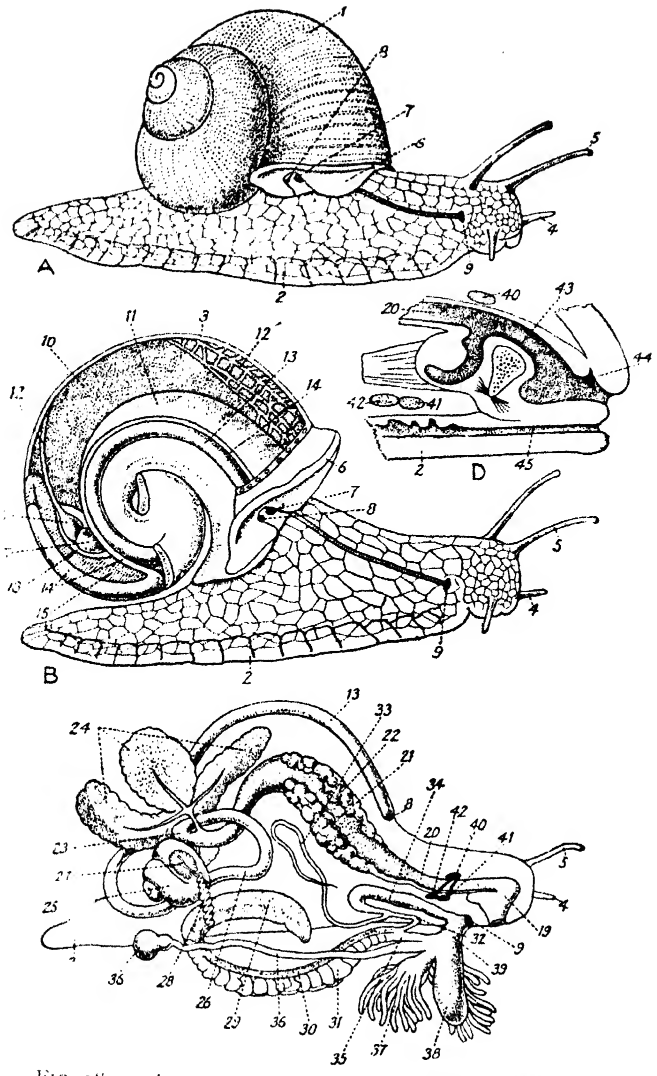


FIG. 18.1.—Anatomy of the edible snail, *Helix pomatia*.

A, View from the right side ; *B*, the same after removal of the shell, part of the mantle, and the upper part of the spiral visceral hump ; *C*, dissection ; *D*, section through buccal mass, enlarged.

1, Shell (note lines of growth) ; 2, foot ; 3, mantle ; 4, anterior tentacle ; 5, posterior tentacle, at the end of which lies a retractile eye ; 6, edge of mantle ('collar') ; 7, opening of lung ; 8, anus ; 9, common genital opening ; 10, mantle cavity or lung ; 11, dorsal wall of body (floor of lung) ; 12, pulmonary vein ; 12', plexus of pulmonary vessels from which pulmonary vein collects ; 13, rectum ; 14, ureter ; 15, kidney ; 16, auricle ; 17, ventricle ; 18, pericardium ; the renopericardial opening (not shown) is near the end of this index-line ; kidney, pericardium, and heart lie in the hinder part of the roof of the mantle cavity ; ureter and rectum run along its right side ; 19, buccal mass, which contains radula ; 20, œsophagus ; 21, crop ; 22, left salivary gland ; 23, stomach ; 24, right liver ; 25, left liver ; 26, intestine ; 27, ovotestis ; 28, hermaphrodite duct ; 29, albumen gland ; 30, male part of compound genital duct ; 31, female part ; 32, vas deferens ; 33, 'flagellum' of penis ; 34, penis (protrusible) ; 35, oviduct ; 36, spermatheca ; 37, 'mucous' glands of uncertain function ; 38, sac of 'love dart' ; 39, vagina ; 40, cerebral ganglia ; 41, pedal ganglia ; 42, viscero-pleural ganglia ; 43, radula (note, behind it, the sac in which it grows, and is pushed forward as it wears away in front) ; 44, jaw ; 45, pedal gland, which secretes the slime of the snail's track.

the front part of the body off the ground and touching-down with the head, the wave of contraction in this case running from head to tail.

THE SHELL

The shell is secreted by the mantle and consists of an outer periostracum, made of an organic material called conchiolin, and two layers largely made of calcium carbonate. The first of these, which is in contact with the periostracum, is the prismatic layer, and inside this is the nacreous layer. The last consists of layers of thin plates of translucent material, set at a slight angle to the surface of the shell, and it is to the interference caused by the reflection of light from these plates that the colours of the inside of the shell are due. They are much more brilliant in some lamellibranchs (p. 284). The shell is a three-dimensional spiral, built round a central axis or columella ; to this is attached the columella muscle, contraction of which pulls the whole animal inside the shell. Most shells are right-handed (dextral) spirals, but about one in a thousand is left-handed (sinistral) ; in these aberrant forms the asymmetry of the body is reversed. In winter, snails become inactive and torpid, often collecting in masses in holes in walls. The opening of the shell is then closed by the epiphragm, a temporary sheet of mucus containing some lime. In many water snails there is a permanent hinged operculum for the same purpose.

TORSION

When the shell is removed, which may sometimes be done merely by unscrewing the animal, although other individuals need to be cut up the shell along the spiral, the mantle and visceral hump are exposed. The latter is covered with a thin skin, from which hangs down the mantle, a thicker extension of skin which is normally raised away from the hump and closely applied to the shell which it has secreted. The lower edge of the mantle, the collar, is fused to the body-wall, so that between the two there is a chamber, the pulmonary cavity, which although inside the shell is outside the body. At the pulmonary aperture the mantle and body-wall are not fused. The main parts of the internal organs have undergone both torsion and coiling, which makes their understanding and dissection difficult. The embryo is at first bilaterally symmetrical, with the anus posterior ; suddenly

the body twists, so that the gut, nerve cords and many other structures are swung to the right and forwards through nearly 180°, and the anus comes to lie just behind the mouth. This is torsion; the dorsal portion then becomes spirally coiled to fit the shell. Torsion is a characteristic and peculiar feature of the Gastropoda (the class to which snails belong) and is developed to different degrees in the various orders.

NUTRITION

Snails feed on leaves, out of which they cut pieces by means of a toothed chitinous tongue or radula (Fig. 18.2), which works

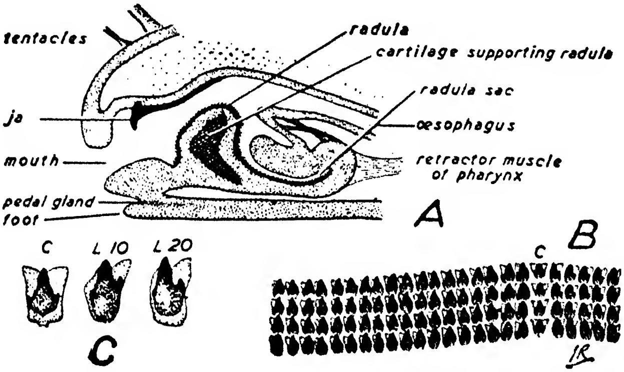


FIG. 18.2.—*Helix pomatia*.—From Thomson.

A, Diagrammatic section of head and buccal mass, showing position of radula and jaw; *B*, portion of four rows of teeth from radula (× 40), each horizontal row contains about 160 teeth and the radula has approximately 160 horizontal rows; *c*, central tooth of row; *C*, three radula teeth (× 170); *c*, central, L 10, L 20, tenth and twentieth lateral.

against a crescentic jawplate on the roof of the mouth. The radula is formed in a radula sac, from which it grows as its front part is worn away. On the dorsal surface of the buccal cavity open two large buccal glands, the secretion of which is a lubricant. From the buccal cavity a short gullet leads back and expands into a large crop, on the dorsal surface of which lie the buccal glands. After the crop comes a short stomach, and then a longer intestine, which is coiled in the dorsal hump and then swings forward on the right side as the rectum to open at the anus behind the mouth. Surrounding the stomach and intestine, and occupying much of the visceral hump, is a structure often called liver, but more accurately known as the digestive diverticula. There are two

lobes, each with its own duct opening into the stomach. Particles of food are carried into the diverticula, and in them most of the digestion as well as most of the absorption takes place, but the secretions are carried forward to the crop, where digestion presumably begins. The finer particles are ingested by the cells of the diverticula, and most, if not all, of the digestion of proteins takes place intracellularly. The snail is one of the few animals to possess an enzyme which can break down cellulose; what is more remarkable is that although it is entirely vegetarian it can also digest chitin.

THE KIDNEY AND CIRCULATION

The ureter, which runs just above the rectum, leads up to a greyish kidney, which produces a variety of nitrogenous products. Its cavity has a minute opening, the renopericardial canal, into the pericardium; the kidney is in fact a cœlomoduct (p. 188). The kidneys should be paired, but the torsion which gastropods undergo has caused the loss of that on the left side.

The pericardium, which, with the renal cavity, is all that is left of the cœlom, lies against the kidney. In it is the heart, consisting of an auricle and a ventricle, which drives blood into an aorta. This divides into an anterior branch to the head and foot, and a posterior to the visceral hump. The finer branches of these arteries open into a system of sinuses, constituting a hæmocœle; this is well seen in dissection, when the dorsal part of the foot is opened, as a large cavity containing the crop and reproductive organs. From the hæmocœle the blood goes to a system of vessels on the roof of the mantle cavity, and so by a pulmonary vein to the auricle. Like the left kidney, the left auricle has been lost. The plasma of the blood contains hæmocyanin, a copper-containing protein which, like the hæmoglobin of vertebrates (p. 528), assists in the transport of oxygen. The floor of the pulmonary cavity is rhythmically raised and lowered by muscles, so that air is drawn in and out.

NERVOUS SYSTEM

All the larger nerves and ganglia are concentrated in the head into a nerve collar which surrounds the gullet. There is a pair of dorsal cerebral ganglia, from which two pairs of nerves run

round the gut to a ventral subœsophageal ganglion ; this represents three pairs of ganglia—pedal, pleural, and visceral—which have fused, although in the swan mussel (p. 280) they are separate. Nerves from the cerebral ganglia go to the mouth and anterior sense organs, and from the other ganglia to the parts of the body suggested by their names. The eye, at the end of the longer tentacle, has a lens-like structure and a retina ; it is especially good at detecting quick movements, as is easily shown if a hand is moved across its field of view, but the range of vision is small. There is a pair of statocysts near the pedal ganglia, and the tentacles are highly sensitive to smell.

REPRODUCTION

The snail is hermaphrodite, and is peculiar in producing both types of gamete in the same gland, which is therefore called an ovotestis. It is a whitish lobed structure at the top of the visceral hump. From it there leads a short coiled hermaphrodite duct, and this passes into a longer common duct, which runs forward. It is incompletely divided into male and female channels. At the junction of hermaphrodite and common ducts is a large albumen gland. The common duct finally divides into a left vas deferens and a right oviduct or vagina. The vas deferens leads into a muscular penis ; just before it does so there is given off a blind diverticulum, the flagellum, which runs back alongside the common duct. The oviduct also gives off a long blind diverticulum or spermatheca, which may be recognised by the subspherical expansion at its end. (This is sometimes called the receptaculum seminis, but this name is better reserved for another structure to be mentioned below.) In *H. aspersa*, but only rarely in *H. pomatia*, the spermatheca itself has a diverticulum, which in dissection is easily confused with the flagellum. Below the spermatheca there opens into the oviduct a lobed mucous gland and below this again the dart sac. Oviduct and penis open together at the common genital aperture. Sperms are produced during most of the year, and are bound together in packets or spermatophores by the secretion of the flagellum. When copulation is about to occur two snails cruise round each other in decreasing circles until, when they are nearly touching, the dart sacs violently contract nearly simultaneously, and from each a calcareous dart is shot into the other snail with enough speed to

penetrate deep into the internal organs. There is a pause after this, and after a time the snails come into close contact, and the penis of each is protruded and inserted into the vagina of the other. The spermatophores are ejected and stored in the spermatheca, where their covering is dissolved and the sperms set free. At some time about June the ovotestis ceases forming sperms and makes ova instead. These are fertilised at the base of the hermaphrodite duct in a small chamber, the receptaculum seminis, by sperms which have swum up the common duct from the spermatheca. The eggs are then surrounded by albumen secreted by the albumen gland, and after passing down the female portion of the common duct, are laid all together in holes in the ground. This happens in July and August. Development is direct, and small snails hatch after about twenty-five days.

SWAN MUSSELS

FRESHWATER mussels may be found in streams, canals, and large ponds in most parts of Britain, though they are often overlooked on account of their habit of burying themselves in the mud with at most a small part of the body projecting. The commonest of them are the swan mussels, *Anodonta cygnea* and *A. anatina*, which differ only in small details of the shape of the shell. When one is removed from the mud it is seen to be enclosed in a flat, dark-green shell, four to six inches long and roughly oval in outline, with one end (the front) rounded and the other more pointed. The shell consists of two similar pieces, known as valves, which lie one on each side of the animal joined by a hinge above the back, where their edges are almost straight. On being disturbed the mussel holds the valves tightly together, but when it is at rest in the water they gape somewhat, and at the hind end, which projects slightly from the mud, there may be seen between them two fleshy lobes enclosing an opening shaped like a figure of 8, through one of whose limbs a current flows into the shell, while through the other, the upper of the two, the water is driven out. At times the animal moves about, thrusting out a yellowish, ploughshare-shaped organ known as the foot, with which it ploughs its way through the mud at the rate of about a mile a year. Freshwater mussels are not unfit for food and are sometimes eaten. They are preyed upon by water-fowl and other

animals, and in places are fished for on account of the pearls which they contain, which may be of considerable value. They are not killed by the freezing of the water even if they themselves be frozen solid, but can survive only a few hours of drought.

SHELL AND MANTLE

The shell has the same layers as in the snail. Lines of growth parallel with its edge mark the outside of the shell (Figs. 18.3, 18.4), centring upon a point about a quarter of its length from the

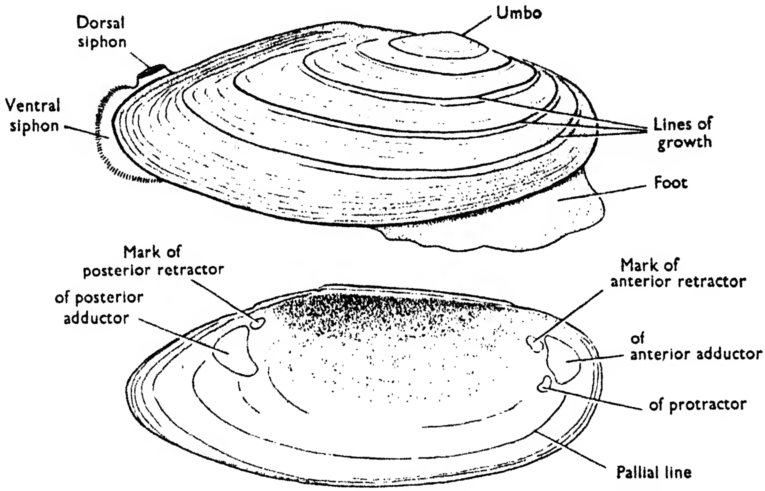


FIG. 18.3.—The swan mussel. Above, a moving animal, from the right side; below, the left valve of the shell, from within.

front end. This point is known as the umbo and shows the position of the first shell of the young mussel. On the inside of the shell may be seen the marks of attachment of the adductor, retractor, and protractor muscles presently to be mentioned, and parallel with its edge is a mark known as the pallial line, where the fold of the body-wall known as the mantle is attached. Above the hinge the two valves are joined by an elastic ligament, which pulls them together and thus causes them to gape below when the adductor muscles are relaxed. To open the shell of a living mussel the handle of a metal scalpel is passed between the valves and they are prised apart; they are then held open, for example by turning the handle at right angles, and the muscles can be cut close to the shell on one side. The body

of the animal is then found to be soft, without a cuticle, and provided with a flap of tissue which hangs down on each side and covers the other organs. This is the mantle (Figs. 18.5, 18.6, 18.7). It has a thick edge which secretes the two outer layers of the shell, while the pearly layer is laid down by the whole outer surface of the mantle and skin of the back. Pearls are formed in the same way in pockets of the mantle surface around foreign bodies which have intruded between mantle and shell. The line of attachment of the mantle from the side of the body is not straight but higher in the middle than near the two ends, though at the extreme ends it turns upwards to the hinge line. At the hind end each mantle edge is fused for some distance with its fellow; it then separates widely from it twice, so as to

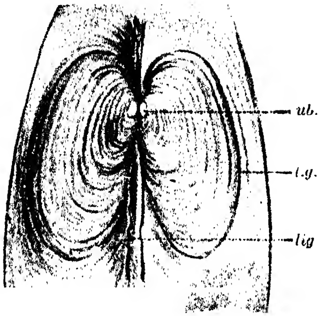


FIG. 18.4.—Part of the shell of a swan mussel, seen from above.

l.g., Lines of growth; *lig.*, ligament; *ub.*, umbo.

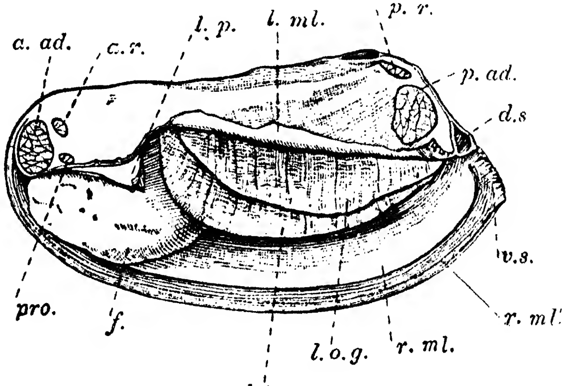


FIG. 18.5.—A swan mussel removed from its shell and lying on its right side with the greater part of the left lobe of the mantle cut away.

a.ad., Anterior adductor muscle; *a.r.*, anterior retractor; *d.s.*, dorsal siphon; *f.*, foot; *l.i.g.*, left inner gill; *l.ml.*, remains of left mantle lobe turned back; *l.o.g.*, left outer gill; *l.p.*, labial palps; *p.ad.*, posterior adductor muscle; *p.r.*, posterior retractor; *pro.*, protractor; *r.ml.*, right mantle lobe; *r.ml'.*, thickened edge of the same; *v.s.*, ventral siphon with papillae.

form the figure of 8 already mentioned, and lies against its fellow for the rest of its length. The upper opening is known as the dorsal siphon, the lower as the ventral siphon. The lips of

the latter bear a fringe of small tentacles. The space enclosed by the two mantle lobes is known as the mantle cavity.

EXTERNAL FEATURES: LOCOMOTION AND FEEDING

It will have been noticed that the shell and mantle of the mussel are bilaterally symmetrical. The same symmetry is found in all the other organs of the body, both internal and external, except for the slightly coiled gut. Above the attachment of the mantle,

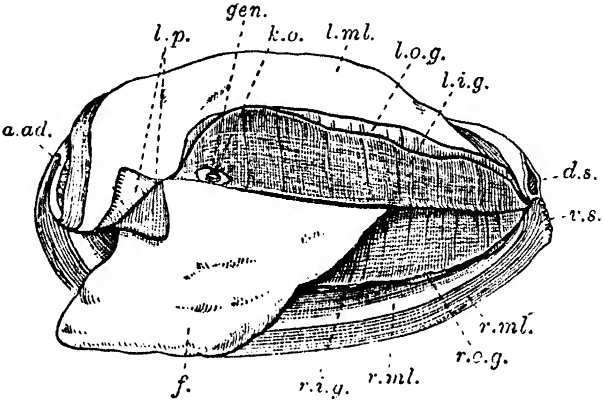


FIG. 18.6.—A swan mussel removed from its shell and lying on its right side with the left mantle lobe and left gills turned back. A portion of the inner lamella of the left inner gill has been cut away to show the openings of the kidney and gonad.

a.ad., Anterior adductor muscle; *d.s.*, dorsal siphon; ., foot; *gen.*, opening of the duct of the gonad *k.o.*, opening of the kidney; *l.i.g.*, left inner gill; *l.ml.*, left mantle lobe; *l.o.g.*, left outer gill; *l.p.*, labial palps; *r.i.g.*, right inner gill; *r.ml.*, right mantle lobe; *r.ml'.*, thickened edge of the same; *r.o.g.*, right outer gill; *v.s.*, ventral siphon.

at its lowest point near each end, may be seen on each side the cut surface of the great adductor muscles, anterior and posterior, which pass through the body from side to side and draw together the valves of the shell. To the upper and inner sides of these lie the anterior and posterior retractor muscles, which draw the body forwards upon the foot when the latter has been thrust out. Behind the lower end of each anterior adductor is a protractor muscle, which draws the body backward upon the foot. If the mantle is turned back the rest of the external organs are laid bare.

At the front and in the middle is a wedge-shaped organ called the foot; its lower part is muscular, and the upper part contains the genital organs and intestine. Blood can be forced into sinuses

which it contains and is prevented from returning by sphincter muscles round the veins; the foot is thus caused to protrude between the valves and to swell, in much the same manner as does the mammalian penis when it is erected. In this state it is wedged into the mud or between the stones at the bottom of the water, and when the retractor muscles contract the body is pulled forwards. The foot is withdrawn by the contraction of its own muscles, which empty the sinuses. Between the foot and the mantle on each side, and extending to the posterior end, are two double flaps called gills, although they have little function as

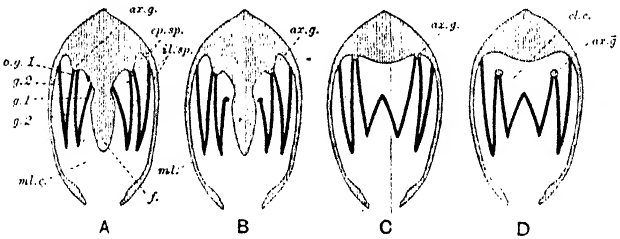


FIG. 18.7.—Diagrams of transverse sections through the swan mussel.

A passes through the middle of the foot and shows the inner lamella of the inner gill attached to the side of the foot; *B* passes through the hinder part of the foot and shows the inner lamella of the inner gill free; *C* is taken behind the foot and shows the inner lamella of the inner gills joining in the middle line; *D* is further back and shows the axes of the gills free.

ax.g., Axes of the gills; *cl.c.*, cloacal chamber; *ep.sp.*, epibranchial space; *f.*, foot; *i.g.1*, inner lamella of inner gill; *i.g.2*, outer lamella of inner gill; *il.sp.*, interlamellar space; *o.g.1*, inner lamella of outer gill; *o.g.2*, outer lamella of outer gill; *ml.*, mantle lobe; *ml.c.*, mantle cavity.

such. At the front end of the foot and also inside the mantle, is another double pair of flaps, the labial palps, which do not in the least resemble the structures of that name in insects. Between the palps lies the mouth; its upper lip joins the outer palps in front of the mantle, and its lower lip joins the inner palps behind.

The structure of the gills is complicated and is shown in Figs. 18.7, 18.8. The general structure of each gill is like that of two sheets of trellis work, joined continuously along the bottom edge, and at intervals elsewhere. Posteriorly the inner lamella of the outer gill, and the whole of the inner gill, become free from the body, although the inner lamellæ of the two inner gills are joined to each other; the result of this is a large space between the gills and the body, which, since the anus opens into it, is called the cloacal space; it opens to the exterior by the dorsal siphon. The mantle, gills, and palps are all covered with cilia of various lengths and direction of beat. These maintain a current of water which comes in at the ventral or inhalent siphon;

particles in the water are sorted by size, some being taken to the mouth, and others rejected through the inhalent siphon. Cilia in the dorsal or exhalant siphon drive out fæces and excreta. The muscular closing of the valves ejects water rapidly from both siphons, and takes place both when the animal is disturbed and when noxious water enters the mantle cavity. The major part of the gas exchange takes place through the surface of the mantle.

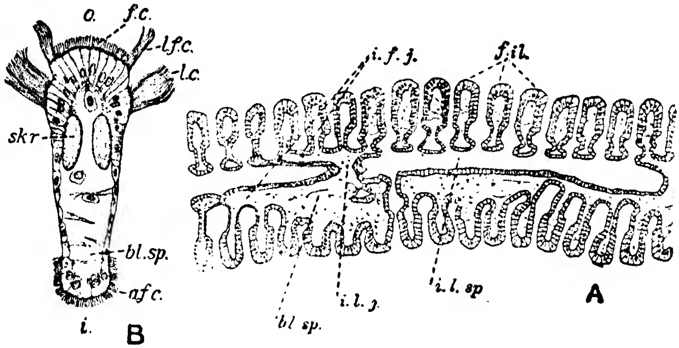


FIG. 18.8.—*A*, A horizontal section through a gill of the swan mussel, under low magnification ; *B*, a single filament of the same, more highly magnified.

af.c., Abfrontal cilia ; *bl.sp.* blood spaces ; *f.c.*, frontal cilia; *fil.*, filaments ; *i.*, side of filament towards interlamellar space ; *i.f.j.*, interfilamentar junction ; *i.l.j.*, interlamellar junction ; *i.l.sp.*, interlamellar space ; *l.c.*, lateral cilia ; *l.f.c.*, laterofrontal cilia ; *o.*, outer side of filament ; *sk.r.*, sections of the chitinous skeletal rods which support each filament.

GENERAL ANATOMY AND ALIMENTARY SYSTEM

The swan mussel is a cœlomate animal, intermediate between the earthworm and the crayfish in respect to its cœlom and hæmocœle. It has a perivisceral cœlom, situated in the back, enclosing the heart and rectum and communicating with the exterior by an excretory tube on each side. This space is the pericardial cavity (Fig. 18.9). In the rest of the body the organs are separated by blood sinuses, the circulation being an open one. The cavity of the gonads represents a part of the cœlom. Most of the viscera lie in the upper part of the body, known as the visceral hump, but the gonads and intestine lie in the soft region of the foot. The mouth leads into a gullet, which passes upwards into a moderate-sized stomach situated behind the anterior adductor muscle. Into the stomach opens by several ducts a series of digestive diverticula, often miscalled a liver ; small particles are circulated through these by cilia, taken up by

the cells, and digested intracellularly. The hinder end of the stomach communicates on the right side with a closed groove of the intestine, the cæcum, which contains a transparent, gelatinous rod, known as the crystalline style (Fig. 18.10). This is composed of a protein substance and projects into the stomach, where it rotates and dissolves. It liberates an amylase which digests carbohydrates; this is the only extracellular digestive enzyme produced by the mussel. The intestine (Figs. 18.11, 18.12) starts from the lower side of the stomach, takes several coils in the soft upper part of the foot, turns upwards, and runs straight backwards in the middle line of the upper part of the body to the anus. The straight part of the intestine is known as the rectum. It lies in the pericardial cavity surrounded by the ventricle of the heart. The ventral wall of the rectum is folded to form a longitudinal ridge or typhlosole. Almost the whole movement of the food in the gut is carried out by cilia.

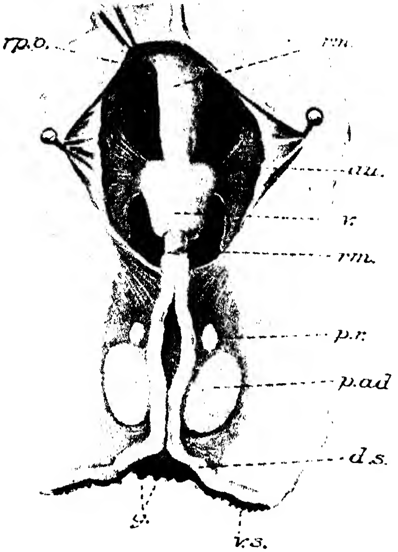


FIG. 18.9.—Part of the dorsal side of a swan mussel in which the pericardial cavity has been opened.

au., Auricle; *d.s.*, margin of dorsal siphon; *g.*, hinder tips of gills, fused to form floor of cloacal chamber; *p.ad.*, posterior adductor muscle; *pr.*, posterior retractor muscle; *rm.*, rectum; *rp.o.*, renopericardial opening; *v.*, ventricle; *v.s.*, margin of ventral siphon opened out by spreading the mantle).

Note between the posterior adductor muscles the fusion of the mantle edges for a short distance, roofing in the cloacal chamber just above the dorsal siphon.

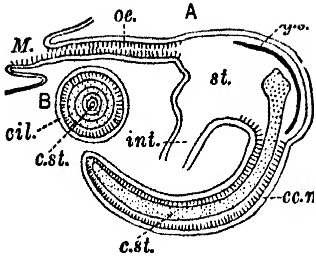


FIG. 18.10.—Sections of part of the alimentary canal of *Donax*.—After Barrois. Yapp, *An Introduction to Animal Physiology*, 1939. Clarendon Press, Oxford.

A, Longitudinal section ; *B*, transverse section of cæcum.

cc.m., cæcum *cil.*, ciliated epithelium ; *c.st.*, crystalline style ; *g.s.*, gastric shield ; ***int.***, intestine *M.*, mouth; *oe.*, œsophagus ; *st.*, stomach.

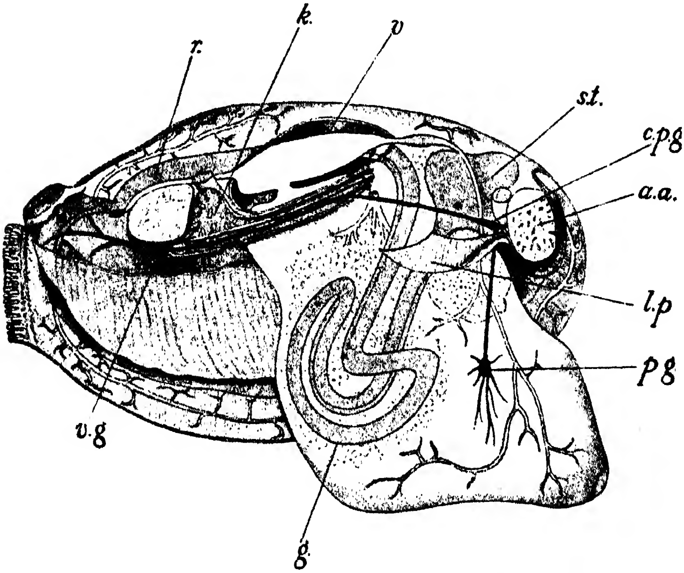


FIG. 18.11.—The structure of *Anodonta*.—After Rankin.

a.a., Anterior adductor ; *c.p.g.*, cerebral or cerebropleural ganglia ; *st.*, stomach ; *v.*, ventricle, with an auricle opening into it ; *k.*, kidney, above which is the posterior retractor of the foot ; *r.*, rectum ending above posterior adductor ; *v.g.*, visceral ganglia with connectives (in black) from cerebropleurals ; *g.*, gut coiling in foot ; *p.g.*, pedal ganglia in foot, where also are seen branches of the anterior aorta and the reproductive organs ; *l.p.*, labial palps behind mouth. At the posterior end the exhalant (upper) and inhalant (lower) siphons are seen.

EXCRETORY ORGANS AND GONADS

The kidneys or organs of Bojanus (Fig. 18.13) are two in number and lie side by side below the pericardium. Each is a wide tube, doubled on itself, with one limb above the other, and the two ends close together in front. The lower limb is glandular and opens

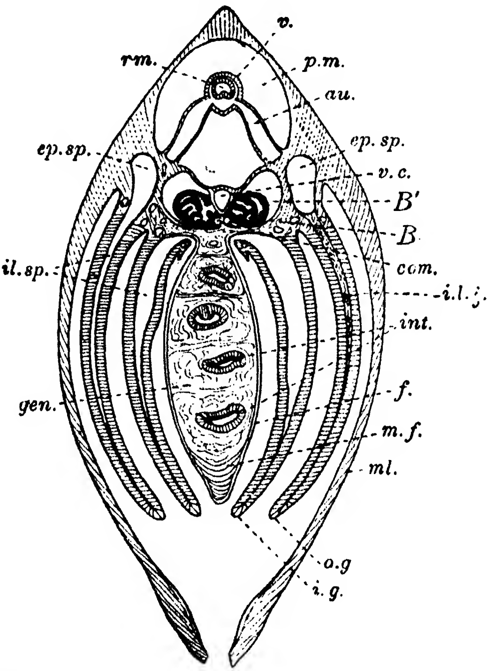


FIG. 18.12.—A semi-diagrammatic drawing of a transverse section of the swan mussel in the region of the hinder part of the foot.

au., Auricle; *B*, glandular limb of kidney; *B'*, non-glandular limb of the same; *com.*, commissure, between cerebral and parietosplanchnic ganglia; *ep.sp.*, epibranchial spaces; *f.*, foot; *gen.*, gonad; *i.g.*, inner gill; *i.l.j.*, interlamellar junction; *il.sp.*, interlamellar spaces; *int.*, intestine; *m.f.*, muscular part of the foot; *ml.*, mantle lobe; *o.g.*, outer gill; *pm.*, pericardial cavity; *rm.*, rectum; *v.*, ventricle; *v.c.*, vena cava.

upwards into the front end of the pericardial cavity by a crescentic renopericardial opening in the floor. The upper limb has thin walls and opens downwards into the space close to the gills shortly before the point at which the inner lamella of the inner gill becomes free. The organ is a cœlomoduct and excretes some nitrogenous material. Cœlomic fluid is drawn by ciliary action through the renopericardial opening into the kidney and is discharged as urine by contractions of the organ. The urine is

of lower concentration than the cœlomic fluid or the blood so that solids must be reabsorbed in the kidney, and the mussel, like other freshwater animals, is continually doing work to prevent itself swelling with water. A pair of glandular bodies known as Keber's organs which lie on each side in front of the pericardium store excreta in their cells. They are derived from the cœlomic wall. The principal nitrogenous excreta are ammonia and amino compounds. The opening of the kidney has thick, yellowish lips. Immediately below it is a somewhat larger opening with thin lips. This belongs to the gonad, which is a branched structure

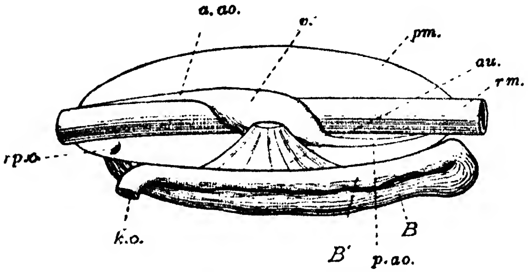


FIG. 18.13.—A diagram of the pericardium and kidney of the swan mussel, from the left side.

a.ao., Anterior aorta *au.*, auricle; *B*, glandular limb of kidney; *B'*, non-glandular limb of the same; *k.o.*, opening of the same; *p.ao.*, posterior aorta; *pm.*, pericardial cavity; *rm.*, rectum; *rp.o.* reno-pericardial opening; *v.*, ventricle.

lying in the upper part of the foot and alike in its general structure in both sexes.

VASCULAR SYSTEM

The blood is colourless and contains white corpuscles. The heart (Fig. 18.13) consists of a ventricle, which is a specialised part of the dorsal aorta which has extended round the rectum and enclosed it, and two auricles, which are triangular, thin-walled structures, one on each side of the ventricle. From the front end of the ventricle an anterior aorta passes forwards above the rectum, and from the hind end a posterior aorta passes backwards below it. From branches of these the blood passes into spaces between the organs. From the foot and viscera it is gathered into a vena cava which lies below the pericardium between the kidneys. Thence it passes outwards through the kidneys to the gills, where it circulates in irregular spaces in the inner parts of the filaments. From these it is returned to the auricles. The blood from the mantle returns direct to the auricles.

NERVOUS SYSTEM

The nervous system (Fig. 18.14) comprises three pairs of ganglia with commissures uniting them. The cerebral ganglia are two

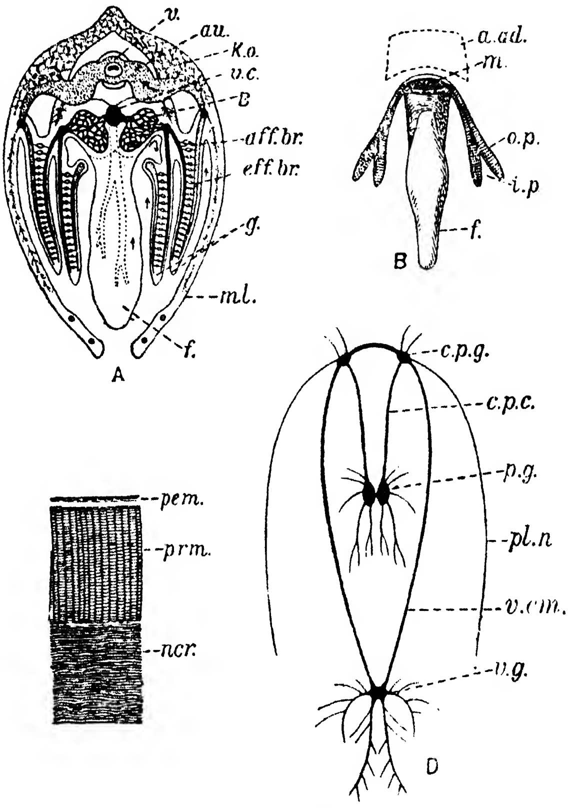


FIG. 18.14.—Details of the anatomy of the swan mussel.

A, Diagram of a transverse section through the foot, showing the principal blood vessels and, by means of arrows, the course of the circulation: each gill is cut at an interlamellar junction.—After Howes. *B*, the mouth and neighbouring structures from in front; *C*, a portion of the shell, in section; *D*, a plan of the nervous system from above, with the visceral commissures more widely parted than they are in the animal.

a.ad., Position of anterior adductor; ***aff.br.***, afferent branchial vessel; ***au.***, auricle; *B*, glandular part of kidney; ***c.p.c.***, cerebropedal commissure; ***c.p.g.***, cerebral (cerebropleural) ganglion; ***eff.br.***, efferent branchial vessels; ***f.***, foot; ***g.***, gills; ***i.p.***, inner labial palp; ***K.o.***, Keber's organ; ***m.***, mouth; ***ml.***, mantle; ***ncr.***, nacreous layer; ***o.p.***, outer labial palp; ***p.g.***, pedal ganglion; ***pem.***, periostracum; ***pl.n.***, pallial nerve; ***prm.***, prismatic layer; ***v.***, ventricle; ***v.c.***, vena cava; ***v.cm.***, visceral commissure; ***v.g.***, visceral (parietosplanchnic) ganglion.

small, orange-coloured bodies, placed one on each side behind the mouth, above which they are connected by a cerebral commissure. They are sometimes known by the name 'cerebro-pleural',

because each contains the elements of two ganglia, the cerebral proper and the pleural, which are distinct in certain other bivalves and in whelks. The cerebral ganglia supply the fore-part of the body, and each gives off a cerebropedal commissure to one of the two pedal ganglia which lie side by side in the foot, just above the muscular region, about one-third of the length of the organ from its front end. The pedal ganglia bear the same relation to the cerebral that the subpharyngeal do to the suprapharyngeal in the earthworm. The pedal ganglia give off several nerves to the foot, and each sends a nerve to a statocyst which lies just behind it. Each cerebral ganglion also gives off a visceral commissure, which runs backwards between the kidneys to join one of the visceral or parietosplanchnic ganglia which lie as a fused pair on the under side of the posterior adductor muscle, immediately within the skin. The sense organs are inconspicuous. They include the statocysts, the tentacles of the ventral siphon, a sensory epithelium, believed to be olfactory, which covers the visceral ganglion and is known as the osphradium, and tactile nerve endings in various parts of the skin. There are no eyes.

LIFE-HISTORY

The sexes of the swan mussel are separate. Semen is passed out through the dorsal siphon and spermatozoa are drawn into the female with the inward stream. The eggs are fertilised in the cloacal chamber and then passed into the space between the lamellæ of the outer gill, where they develop. This takes place in the summer. In the following spring the young are set free. They are larvæ, very unlike the parent, and are known as glochidia (Figs. 18.15, 18.16). Each has a shell composed of two triangular valves, hinged along the base and with the apex drawn out into a strong hook. There is no posterior adductor muscle, anus, or foot, but in the place of the latter is a gland which secretes a long sticky thread known as the byssus, comparable with the threads by which the adult sea mussel anchors itself. When some small fish, such as a stickleback, passes over the glochidium, the latter flaps its valves so as to drive out the byssus, which if it touches the fish sticks to it. The movements of the fish now bring the glochidium against its body, whereupon the hooks are used to hold on to its skin. The tissues of the fish become inflamed and swell up, enclosing the little parasite, which lives for some

months by absorbing the juices of its host, during which time it undergoes a change into the adult form. Eventually the skin

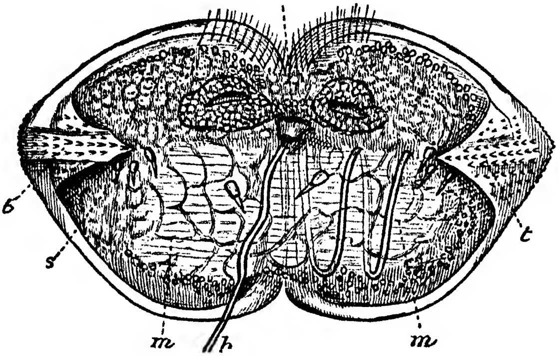


FIG. 18.15.—A glochidium larva in ventral view.—From Latter.

b., Byssus (cut short) ; *d.*, future mouth ; *m.*, adductor muscle ; *s.*, sensory cells ; *t.*, main teeth and denticles on ventral edge of each valve.

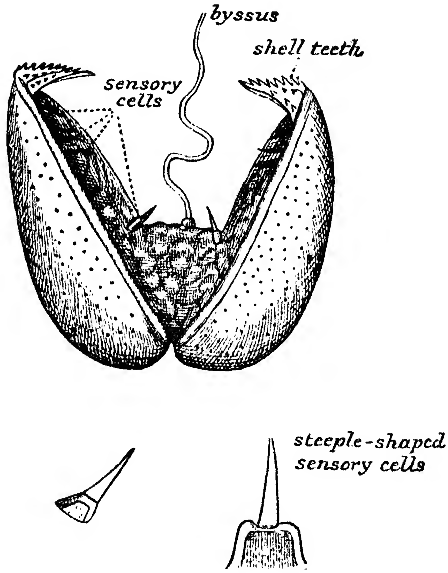


FIG. 18.16.—A glochidium larva, as cast out from the parent, viewed from behind.—From Latter.

enclosing the young mussel withers and it drops off to lead an independent life. By means of this larva, the slow-moving mussel is dispersed into fresh feeding grounds by the fish, without

the risk, which would be considerable if so small a larva were free-swimming, of being carried downstream to the sea. We have seen that the young of the crayfish escape the same danger by holding on to the body of their mother. It is interesting to note that marine relations of both these animals have free-swimming larvæ, and to recall that *Hydra* lacks the free larva of the sea-dwelling *Obelia*.

MOLLUSCA

The snail and the swan mussel illustrate pretty well the general features of the phylum Mollusca. Though cœlomate, the animals

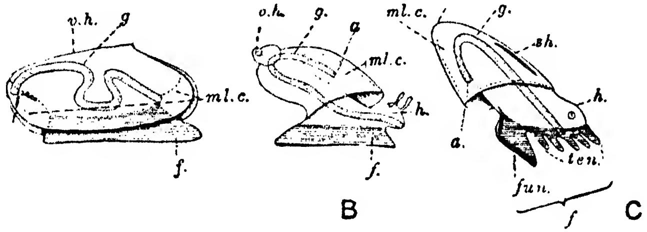


FIG. 18.17.—Diagrams of a mussel (A), a whelk (B), and a cuttlefish (C).—Partly after Lankester.

a., Anus ; *f.*, foot ; *fun.*, funnel through which water is squirted by the cuttlefish in swimming ; *g.*, gut ; *h.*, head ; *ml.c.*, mantle cavity ; *sh.*, internal shell found in some cuttlefish (the "cuttle bone"); *ten.*, tentacles of the cuttlefish ; *v.h.*, apex of visceral hump.

of this phylum have usually a functional hæmocœle, the cœlom being reduced to the cavity of the gonads. They are the most complex of unsegmented animals. There are three unique features found in various forms in the different classes (Fig. 18.17), but with little resemblance to anything found elsewhere : the ventral and largely muscular foot, a dorsal visceral mass, and, covering this and hanging down from it to enclose a cavity, a special skin called the mantle. A shell is often but not invariably secreted by this. The typical larva of the molluscs (not seen in either of our examples) is a trochophore very similar to that of the annelids. Intracellular digestion is common. There are five classes.

CLASS I—AMPHINEURA

These are primitive forms with a poorly developed head, and spicules in the mantle. *Chiton* (Fig. 18.18) is somewhat limpet-like, but has eight transverse shell-plates, and is marine.

CLASS II—GASTROPODA

The head is moderately well developed, with tentacles and eyes; the foot is more or less flattened dorsoventrally, and the visceral mass has undergone the torsion described above (p. 266) so that there is some degree of asymmetry. There is usually a shell in a single piece and a radula is present. The snail illustrates these general characters, but is atypical in that it and its relatives which live on land or in fresh water (the Pulmonata) have lost some features and developed new ones. The majority of gastropods are marine, and have gills (ctenidia) in the mantle cavity and a trochophore larva. In many the sexes are separate. The limpet *Patella* has a shell with very slight coiling and is herbivorous; the dog-whelk, *Buccinum*, like a large pointed snail, is carnivorous.

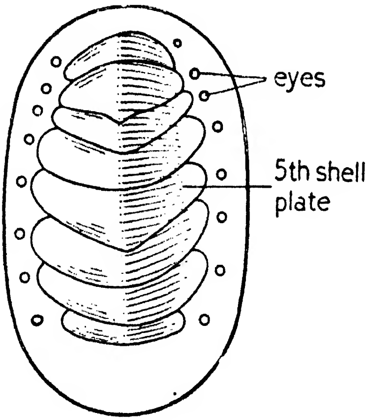


FIG. 18.18.—*Chiton*, dorsal view.

CLASS III—SCAPHOPODA

This is a small order of bilaterally symmetrical molluscs with a tubular shell open at both ends. That of *Dentalium* is common on the shore.

CLASS IV—LAMELLIBRANCHIATA

These are bilaterally symmetrical and compressed animals with a large mantle in two flaps. Each of these secretes its own portion of the shell, so that this is bivalved, the two parts being connected by a hinge. This bivalve construction determines, or is determined by, the rest of the arrangement of the body, and the whole mode of life; there are special muscles to close the shell, and an elaborate arrangement of cilia on the gills and mantle for feeding on small particles. The labial palps border the mouth. The swan mussel shows the general characters, but most members of the class are marine, have the sexes separate, and have a trochophore larva.

CLASS V—CEPHALOPODA

The cuttlefish are peculiar and specialised molluscs of great muscular development and activity, not easily related to the other groups. The foot is modified as a funnel by and through which water is expelled to drive the animal vigorously backwards. The pelagic forms have horizontal lateral fins by which they swim forwards. Alone among animals, except perhaps for man and the great apes, the cephalopods have a head which is not the first part of the body to meet the external world. It has a high concentration of nervous tissue, and large and well-developed eyes Surrounding the brain there is a skull of a material resembling cartilage and rich in collagen, which is also found stiffening the fins and tentacles. The mouth has a radula and is surrounded by eight or ten long muscular tentacles, possibly part of the foot. The cœlom is often well developed and the development is direct.

Besides the cuttlefish, which have either an internal shell (*Sepia*) or none (*Octopus*) the class includes *Nautilus*, with a spiral-chambered shell, and many extinct forms (including the ammonites) also with shells.

19

THE STARFISH

EXTERNAL FEATURES

ONE of the most familiar animals of the seashore is the common starfish, *Asterias rubens*. It may often be found dead or dying

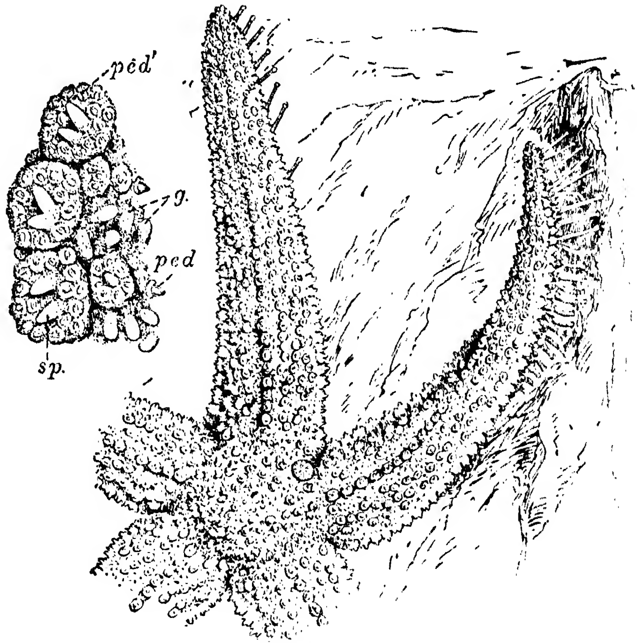


FIG. 19.1.—Part of an aboral view of a starfish (*Asterias rubens*) and an enlargement of a small part of the surface of the same.

g., Gills ; *ped.*, large pedicellaria ; *ped'.*, small pedicellaria ; *sp.*, spine.

upon the beach where it has been thrown up, or living in pools, but its principal haunts are in somewhat deeper water. For all its seeming helplessness, it is an exceedingly voracious animal, and is particularly destructive to shellfish, so that it is a pest in oyster beds. Its body, of a colour varying from orange to purplish, and darker above than below, has the shape of a star, with five tapering rays, or arms, meeting in a central region known as the disc. The upper side is called aboral (Fig. 19.1), the lower oral (Fig. 19.2), because on it, in the middle of the disc, lies the mouth, The direction of each arm is known as a radius. The

region between two arms is an interradius. Along each arm runs on the oral side a deep ambulacral groove, and the grooves meet around the mouth, which has a membranous lip or peristome.

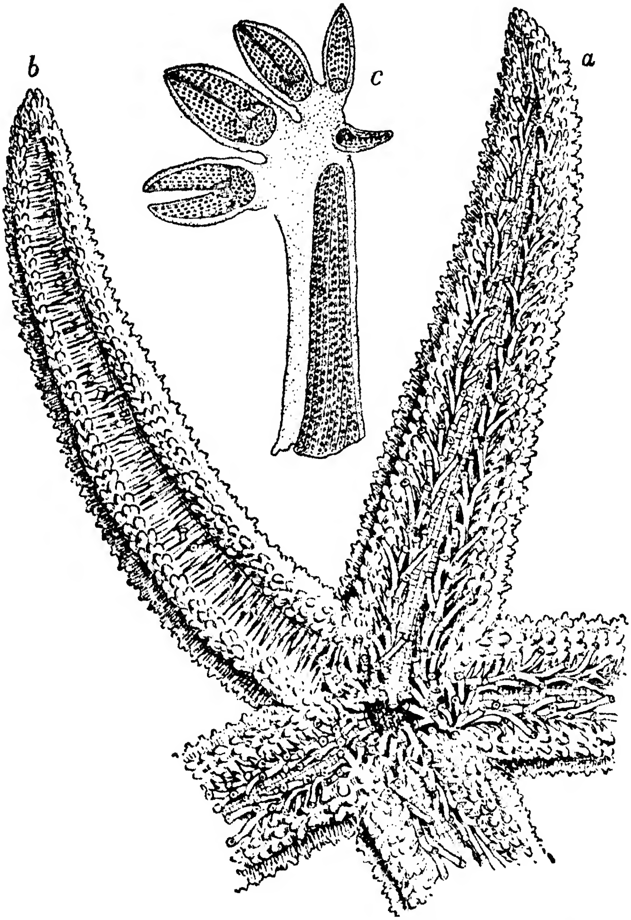


FIG. 19.2.—Parts of an oral view of a starfish (*Asterias rubens*).

a, An arm with the ambulacral groove widely open ; *b* an arm with the ambulacral groove closed by the contraction of its sides and the bending over of the adambulacral spines ; *c*, an ambulacral spine, with its tuft of large pedicellariæ enlarged.

The surface of the body is soft and ciliated, but below it is a tough body-wall, strengthened by a meshwork of rod-shaped calcareous ossicles, which can be felt and seen through it. Over the interspaces between the ossicles the skin is raised into delicate, hollow outgrowths, the dermal gills, into which the body cavity

is prolonged. From the junctions of the ossicles arise blunt spines, each of which is surrounded by a cushion of skin. Crowded upon these cushions, and scattered between them, are remarkable little organs known as pedicellariæ, each of which is a minute pair of pincers, supported by little ossicles, one at its base and one in each jaw. The pedicellariæ are defensive organs. They are of two kinds, a smaller kind, found upon the cushions of the spines of the back, in which the supporting ossicles cross at the base like the blades of a pair of scissors, and a larger kind, scattered between the spines, whose ossicles do not cross. In an interradius, on the aboral surface, is a conspicuous button-like ossicle, covered with fine grooves, and known, from its coral-like appearance, as the madreporite. Its grooves are pierced with fine pores through which, by the action of cilia, water is drawn in. The anus is a small opening, almost in the middle of the aboral surface, but slightly displaced towards the interradius next (clockwise) to that in which the madreporite lies. Each ambulacral groove is crowded with tube-feet, delicate, cylindrical tentacles, ending each in a sucker, set in four rows. It is by these that the animal crawls, and they are also used to hold prey. At the sides of the ambulacral grooves stand a number of adambulacral spines, which bear pedicellariæ of the uncrossed kind and can be brought together over the groove so as to protect the tube-feet. At the bottom of the groove a longitudinal nerve ridge marks the position of a radial nerve cord. At the end of the groove is a single sense-tentacle, like a tube-foot but smaller and without sucker, which subserves the olfactory sense and has at its base a red eye-spot.

BODY-WALL, NERVOUS SYSTEM, AND CŒLOM

Below the epithelium with which the body is covered is a dense network or plexus of nerve fibres. It is thickened to form a ring round the mouth, and from this a radial nerve, in which many of the fibres run longitudinally, extends down each arm to end in the sense tentacle. Another network, with which the first communicates, lies in the wall of the cœlom. Below the epithelium, the body-wall is composed of connective tissue, in which the ossicles are embedded. The deeper part contains some muscular fibres in various directions. A large cœlom, lined with ciliated epithelium, surrounds the alimentary canal and generative organs. and extends into the arms. In each interradius a stiff interradial

septum projects into the cœlom between the arms. To the septum which is situated in the interradius of the madreporite there is attached a sac, the axial sinus, also a part of the cœlom, and in this are lodged the stone canal, which, as will presently be stated, runs downwards from the madreporite, and a spongy, brown organ, the axial organ, to which also we shall return.

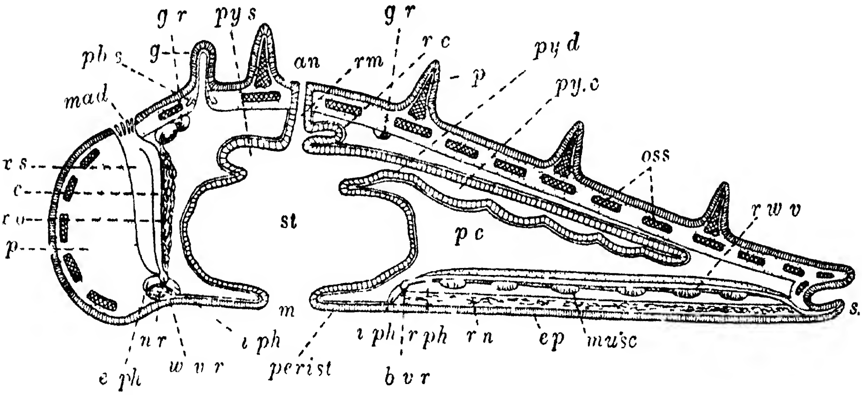


FIG. 19.3. Diagram of a section of a starfish passing through the madreporic interradius and along the opposite arm, a little to one side of the septum of the radial perihæmal vessel.

an, Anus; *ax. o*, axial organ; *ax. s*, axial sinus; *b l r*, ring of lacunar tissue; *ep*, epidermis; *g*, gill; *g r*, genital rachis; *in an*, aboral cœlomic ring sinus; *i ph*, inner perihæmal ring; *m*, mouth; *mad*, madreporite; *musc*, one of the muscles that narrow the ambulacral groove; *n r*, nerve ring; *o ph*, outer perihæmal ring; *oss*, ossicles; *p c*, perivisceral cavity; *ph s*, peribranchial sinus; *perist*, peristome; *py c*, pyloric cæcum; *py d*, pyloric duct; *py s*, pyloric sac; *r c*, rectal cæcum; *r m*, rectum; *r n*, radial nerve; *r ph*, radial perihæmal vessel; *r w v*, radial water vessel; *sep*, septum; *sp*, spine; *st*, stomach; *st c*, stone canal; *s t*, sense tentacle; *w v r*, water vascular ring.

ALIMENTARY CANAL, FEEDING, AND EXCRETION

The mouth opens through a short œsophagus into a great sac, the stomach (Figs. 19.3, 19.4), which has in each interradius a wide pouch, attached to the ambulacral ridge by two retractor muscles. Above, the stomach communicates by a wide opening with a five-sided pyloric sac, each angle of which is prolonged into a tube or pyloric duct, that runs into an arm, and there forks into two branches, the pyloric cæca, each beset with numerous little pouches and slung from the aboral wall of the arm. From the pyloric sac a short, conical rectum leads to the anus. It bears interradially two small brown branches, the rectal cæca. The starfish will eat any animal that it can master. Small prey may be taken into the mouth, but usually digestion is performed in a remarkable manner outside the body ; the arms bend round the

prey and hold it with their tube-feet, while the stomach is forced out, by contraction of the body-wall compressing the cœlomic

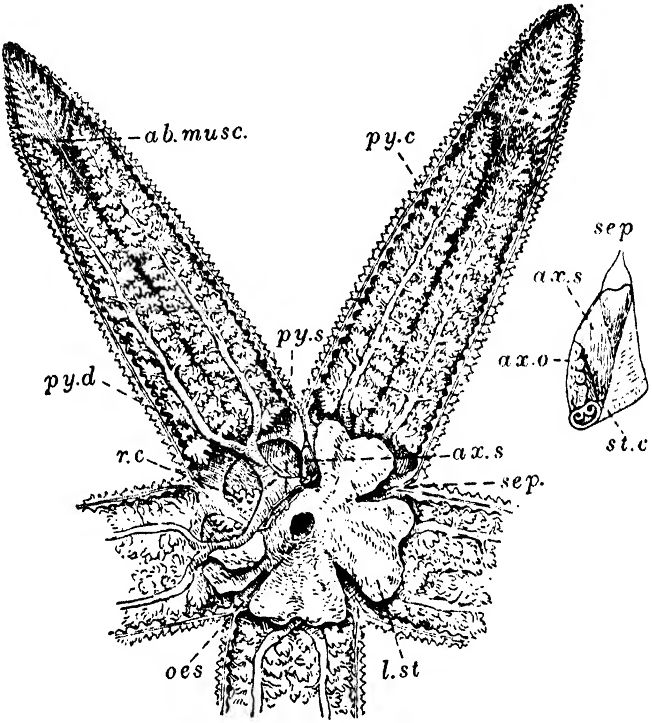


FIG. 19.4.—Parts of the aboral half of a starfish (*Asterias rubens*), removed, with the alimentary canal, from the rest of the body, and viewed from within. One lobe of the stomach has been cut away, and another partly turned back. The detached figure represents an enlarged view of the axial sinus and adjoining structures.

ab.musc., Aboral muscle; *ax.o.*, axial organ; *ax.s.*, axial sinus; *l.st.*, one of the lobes of the stomach; *oes.*, œsophagus; *py.c.*, pyloric cæcum; *py.d.*, pyloric duct; *py.s.*, pyloric sac; *r.c.*, rectal cæcum; *sep.*, septum; *st.c.*, stone canal.

fluid, and enwraps the prey. Enzymes are secreted on to the food, and when digestion is complete the stomach is withdrawn by the retractor muscles. In eating bivalves, which are a great part of its food, the starfish brings two arms over one of the valves and three on to the other, and attaches them by the tube-feet; the valves are then pulled apart, and the stomach is inserted into the shell. The digestive juice is secreted by the cells which line the pyloric cæca. Shells are left behind by the stomach, or rejected through the mouth, very little matter being cast out through the anus. The fluid of the water vascular system contains

small quantities of ammonia, amino compounds, and urea, and since it is in communication with the surrounding seawater, nitrogen is presumably lost from it. Similar excreta are said also to be got rid of through the walls of the gills, partly in solution, partly as granules carried by amœboid cells which pass through to the exterior. The rectal cæca appear also to excrete waste matter, which passes out by the anus. The starfish is strictly stenohaline (p. 193), being unable to live except in the sea.

WATER VASCULAR SYSTEM

The working of the tube-feet is brought about by a peculiar system of tubes, derived during development from the cœlom, known as the water vascular system (Fig. 19.5). This starts at the madreporite as the stone canal, so called because it is strengthened by calcareous matter. The wall of this canal makes a curious projection into it, Y-shaped in section, with the arms of the Y rolled, so that the surface is greatly increased, and it is ciliated. The lower end of the stone canal joins a ring canal around the mouth, above the peristome, and from this a radial canal runs down each arm, below the ambulacral ossicles. From the radial canals small transverse canals run, one to each tube-foot. The hollow of the tube-foot is prolonged inwards into a bulb called the ampulla, which projects into the cœlom of the arm. The transverse canal joins it just below the ampulla, by a valved opening which prevents fluid from flowing into the radial canal, so that, when (by a circular muscle layer) the ampulla contracts, the fluid in it stretches out the tube-foot. Muscles in the foot direct it against the ground, by cupping the sucker cause it to adhere, and then shorten the foot, so that it tends to draw the body forward. Owing to the shortening of the foot the fluid passes back to the ampulla. The pressure of the fluid in the water vascular system is regulated by gain, and perhaps also by loss, of water through the madreporite.

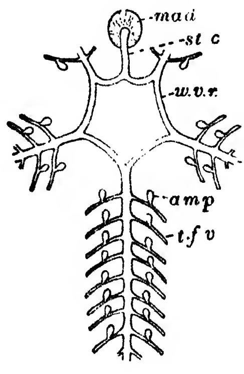


FIG. 19.5.—A diagram of the water vascular system of a starfish.

amp., Ampulla; *mad.*, madreporite; *r.w.v.*, radial water vessel; *st.c.*, stone canal; *t.f.v.*, vessel of tube foot; *w.v.r.*, water vascular ring.

PERIHÆMAL AND PSEUDOHÆMAL SYSTEMS

The radial water vessel in each arm lies close under the ambulacral ossicles ; below it there is a cœlomic space, roughly diamond-shaped in transverse section, which is known as the radial perihæmal cavity. Below the perihæmal cavity the epidermis is thickened by an increase in the nerve plexus, and folded so as to project into the ambulacral groove as the nerve ridge. Round

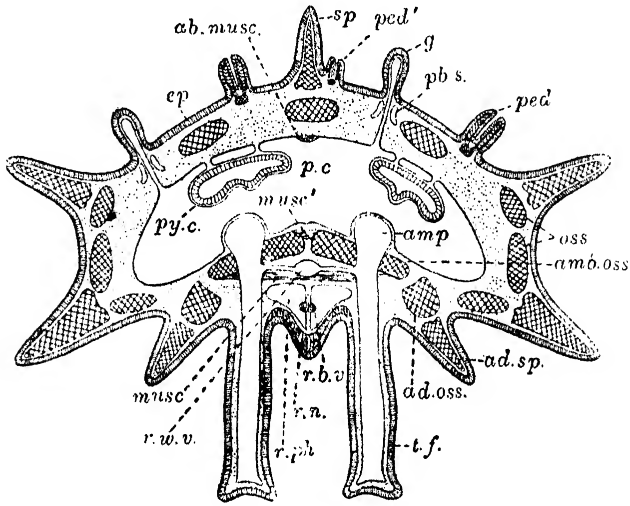


FIG. 19.6.—Diagram of a transverse section of the arm of a starfish.

ab.musc., Muscle which straightens the arm ; *ad.oss.*, adambulacral ossicle ; *ad.sp.*, adambulacral spine ; *amb.oss.*, ambulacral ossicle ; *amp.*, ampulla of tube foot ; *ep.*, epidermis ; *g.*, gill ; *musc.*, muscle that narrows the ambulacral groove ; *musc'.*, muscle that opens the ambulacral groove ; *oss.*, ossicles ; *pb.s.*, peribranchial sinus ; *p.c.*, perivisceral cavity ; *ped.* and *ped'.*, pedicellariæ ; *py.c.*, pyloric caecum ; *r.b.v.*, radial 'blood vessel' ; *r.n.*, radial nerve ; *r.ph.*, radial perihæmal vessel ; *r.w.v.*, radial water vessel ; *sp.*, spine ; *t.f.*, tube-foot.

the mouth, the radial perihæmal vessels are joined by an oral perihæmal ring.[1] Each radial vessel is divided longitudinally by a vertical septum, and in this septum lies a strand of a lacunar tissue which in the starfish takes the place of the blood vessels. This is a part of the connective tissue in which the fibres are more sparse and the ground substance more fluid than elsewhere, and it is believed that along the strands which are formed of it substances diffuse, and amœboid cells wander, more readily than elsewhere. Around the mouth a ring strand joins the radial strands, with this is connected the tissue of the axial organ, and

[1] Adjoining this is another cœlomic tube, the so-called 'inner perihæmal ring', which is connected not with the perihæmal vessels but with the axial sinus.

with the aboral end of the axial organ is again connected an aboral ring, from which strands extend to the generative organs.

REPRODUCTION

The axial organ, however, is primarily of importance, not as a part of this 'pseudohæmal system', but as the original seat of the genital cells, for which reason it is often known as the 'genital stolon', while the aboral ring is the 'genital rachis'. Along the latter the genital cells wander from the stolon to the actual gonads. These are ten in number, shaped like bunches of grapes, and varying in size with the season of the year. They are attached to the body-wall by their ducts, which open one on each side of the base of each arm, towards the oral aspect. The sexes are separate, but do not differ externally. Eggs and

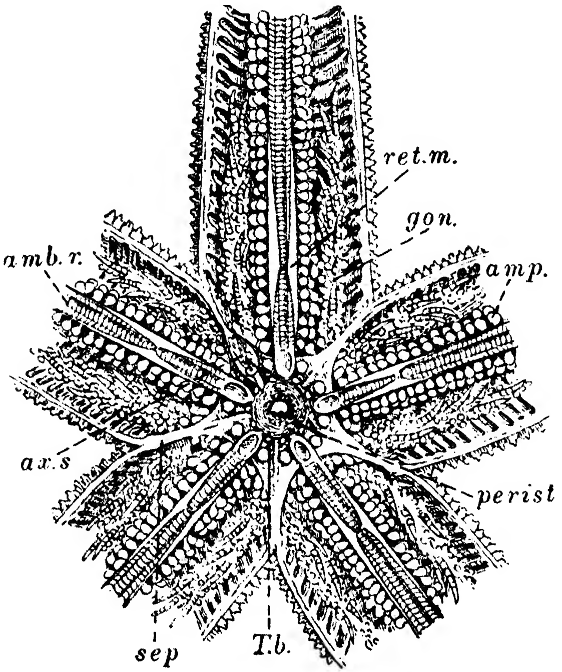


FIG. 19.7.—Part of a view from above of the oral half of a starfish (*Asterias rubens*), after removal of the alimentary canal.

amb.r. Ambulacral ridge; *amp.*, ampullæ of tube-feet; *ax.s.*, axial sinus, with stone canal and axial organ *gon.*, generative organ; *perist.*, peristome; *ret.m.*, retractor muscle of the stomach; *sep.*, septum; *T.b.*, Tiedemann's body.

sperms are shed into the water, where fertilisation takes place. The cleavage of the ovum is complete and practically equal. It leads to the formation of a remarkable, bilaterally symmetrical larva (the bipinnaria, Fig. 19.8), which swims by two bands of cilia. This, after passing through a fixed stage, the brachiolaria, gives rise to the radially symmetrical adult, through a peculiar metamorphosis, in which its left and right sides become the oral and aboral surfaces.

BEHAVIOUR

Like most animals the starfish moves towards the side from which certain stimuli come. In crawling one (or sometimes two) of the arms is directed forwards. On this leading arm each tube-foot—not moving in step with any other—is extended in the direction of the arm, makes contact with the ground, and then swings back, so that it moves the body forwards like the legs of other animals. On a vertical surface, or when a starfish meets a resistance, the foot acts as a sucker, and the animal is pulled forwards. On the other arms the tube-feet behave in the same manner but swing to and fro in the direction in which the animal is crawling—that is, more or less transversely to their arms. A starfish which falls on its back can right itself. In this process also one or two arms take the lead, turning over so as to touch the ground and holding on with their tube-feet, while the other arms, probably stimulated by the first movers, arch over by muscular action till the creature topples over on to its oral side. The arms which take the lead are those which had previously led in crawling. Pedicellariæ bend towards the site of a gentle stimulus on the skin, opening their blades and closing them upon any object that comes against their inner sides. The larger kind are set in motion by a weaker stimulus than is needed to move the smaller ones; these are brought into position for action by the rising of the cushions upon which they stand. If the ambulacral

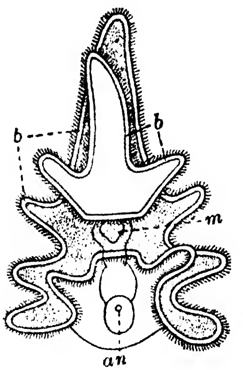


FIG. 19.8.—The bipinnaria larva of a starfish, in ventral view.

an., Anus; *b.*, postoral ciliated band; *b'.*, preoral band; *m.*, mouth.

The depressed region between the ciliated bands is shaded.

groove be touched the adambulacral spines come together over it.

The movements of the tube-feet are co-ordinated by the deep nerve tracts. At the base of each arm is a centre which normally causes the feet of that arm to point towards its tip, which is the stable position, but on the receipt of a stimulus one of the five centres becomes dominant, and impulses are sent round the nerve-ring and along the radial tracts to cause all the tube-feet to point and swing in the same plane. Conduction of the impulses is decremental, so that an impulse caused by a weak stimulus may die out before it reaches the other arms, and one of these may in turn become dominant. The movements of the pedicellariæ and spines are controlled by local impulses in the superficial nerve net. This can also cause the tube-feet to respond to strong stimuli.

ECHINODERMATA

The starfish is an example of the phylum Echinodermata, a peculiar group which shows a mixture of primitive and highly

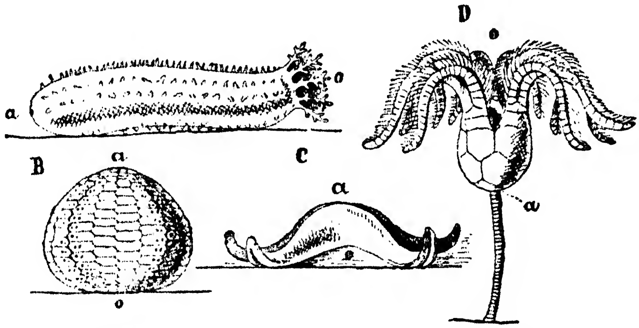


FIG. 19.9.—Semi-diagrammatic views of a starfish (*C*), a sea urchin (*B*), a holothurian (*A*), and a crinoid (*D*), in the natural position.—From Lang.
a, Aboral side ; *o*, oral side.

specialised characters. They are triploblastic and cœlomate, but have no blood system and the nervous system is a nerve net. The water vascular system, a specialised part of the cœlom, is associated with the peculiar method of locomotion by tube-feet, but is also excretory and perhaps respiratory in function. There are various peculiar types of larva, which are bilaterally symmetrical, but the adults have a secondary radial symmetry, replaced in one class by a tertiary bilateral symmetry. The original plane of bilateral symmetry is marked by the madreporite. The

echinoderms, alone among invertebrates, have a mesodermal skeleton which consists of calcareous ossicles. In this skeleton, in some points of embryology, and in some of biochemistry, they show resemblances to the chordates. The substitution of radial for bilateral symmetry is perhaps connected with ancestors which were all sessile, as some modern adults and many larvæ still are. There are five existing classes, and some which are extinct. All existing echinoderms are marine, and members of the phylum were common in palæozoic times.

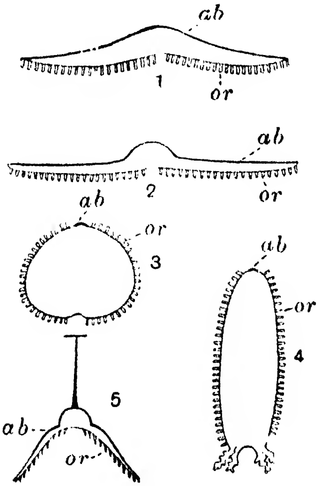


FIG. 19.10. Diagrams to show the relative extent of the oral and aboral surfaces, and to compare the form of body, in the several classes of Echinodermata. The diagrams are in the same morphological position.

1, Asteroidea; 2, Ophiuroidea; 3, Echinoidea; 4, Holothuroidea; 5, Crinoidea.
ab., aboral surface; *or.*, oral surface.

CLASS I—ASTEROIDEA

The starfishes are adequately represented by *Asterias*. The shape is characteristic—a five-pointed star, in which the rays of the star are not sharply marked off from the disc. The diverticula of the gut extend into the arms, the ambulacral grooves are open, and the sucker-type tube-feet and pedicellariæ are usually present. The madreporite is aboral. In some the number of arms is increased, occasionally to as many as 45; a few have only 4.

CLASS II—OPHIUROIDEA

In these, the brittle stars, the arms are clearly marked off from the disc, so that the star-shape is lost. The other characters are also the opposite of those of the starfish; the gut diverticula do not extend into the arms, the ambulacral groove is covered, the tube-feet have no suckers, and there are no pedicellariæ. The madreporite is oval. *Ophiothrix* is one of the commoner British genera.

CLASS III—ECHINOIDEA

The sea urchins are more or less globular, without arms. The adambulacral area is greatly extended to form the sides as well as the base of the globe; the abambulacral area is confined

to a small polar region round the madreporite. The ambulacral grooves are covered, the tube-feet have suckers, pedicellariæ are present, and there are spines. The skeleton usually makes a rigid box of calcareous plates. Most of the volume of a sea urchin is taken up by the body cavity, in which the spiral gut is slung. A common example is *Echinus esculentus* of British coasts. Some, such as *Spatangus*, are heart-shaped, with slight bilateral symmetry.

CLASS IV—HOLOTHUROIDEA

The sea cucumbers bear a superficial resemblance to the vegetables of the same name. The body is elongated in the direction from anus to mouth, which opens towards the direction in which the animal moves, so that there is a tertiary bilateral symmetry. The adambulacral area is reduced and the madreporite usually internal. The ambulacral grooves are covered, some tube-feet have suckers and others are modified into oral tentacles. There are neither spines nor pedicellariæ. The skeleton is reduced and the skin leathery in texture. *Holothuria* is a common genus.

CLASS V—CRINOIDEA

The sea-lilies, or feather stars, resemble most of the fossil forms in being, for at least part of their life, sessile by a stalk which grows from the aboral side. The arms, which are sharply marked off from the disc, are branched. The ambulacral grooves are open, the tube-feet have no suckers, and there are neither pedicellariæ nor spines. There is no madreporite. *Rhizocrinus* is a deep-water form with a long permanent stalk. *Antedon rosacea* lives at about ten fathoms, and when adult breaks loose and swims by waving its arms. Round the stump of the stalk is a ring of cirri, which are used for temporary attachment.

20

THE LANCELET

HABITS AND EXTERNAL FEATURES

THE common lancelet *Branchiostoma lanceolatum* (=*Amphioxus lanceolatus*), is a little, fish-like creature found on most European coasts, including those of Britain, living in shallow water on a sandy bottom. It passes most of its time buried in the sand, with its long axis upright and the fore-end projecting, gathering small organisms for food by a ciliated apparatus round the mouth.

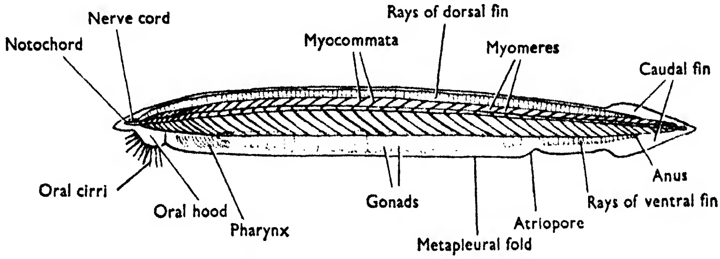


FIG. 20.1.—The lancelet, from the left side, with the atrial floor contracted. × 1.5.

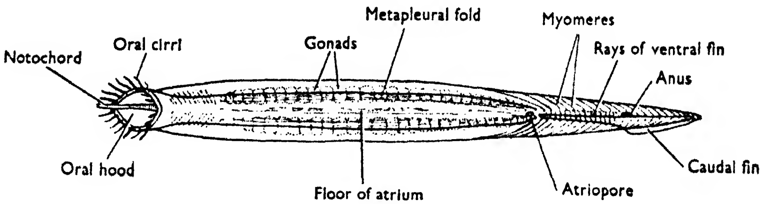


FIG. 20.2.—The lancelet. Ventral view. × 1.5.

From time to time, usually at night, it leaves the sand, and then swims by movements of its muscular body, turning clockwise (as seen from behind) as it does so. It is about an inch and a half long, lustrous but translucent, slender, pointed at each end, and flattened from side to side. The external features, and so much of the general structure as can be seen without dissection, are shown in Figs. 20.1 and 20.2. The mouth is on the ventral surface a little way back from the anterior end and is surrounded by the oral

hood, whose edge is produced into a number of ciliated tentacles or oral cirri, and the anus, also ventral and a little to the left, is a slightly greater distance forward from the posterior end. The exterior of the body beyond the anus, containing no part of the gut, is called the tail. A continuous unpaired fin begins as the right edge of the oral hood, runs up round the anterior end of the body, backward as a low median dorsal fin, round the tail as an expanded caudal fin, and forward again as a ventral fin for about one third the length of the body, ending at an opening called the atriopore. In front of the ventral fin the belly is flattened and bears at each side a continuous lateral fin or metapleural fold. About sixty myocommata and muscles (see below) make a V-shaped pattern on the sides of the body, about seven being in front of the mouth. Certain of the internal organs are repeated in correspondence with these myomeres, so that the body is segmented, though not so completely as that of the earthworm. The segmentation is peculiar in that the myomeres of opposite sides alternate.

ATRIUM

The atriopore leads from a large cavity (best seen in a transverse section, Fig. 20.3) which lies below and at the sides of the middle part of the body and is known as the atrium. This cavity is not really within the body, but is enclosed between the body and two longitudinal folds of the body-wall, the metapleural folds, like those which form the branchiostegites of the crayfish, save that they meet in the middle line below, leaving at their hinder end an opening which is the atriopore. The atrium communicates with the pharynx by a number of slits at each side, known as the gill slits. The atrium is prolonged backwards on the right side behind the atriopore almost as far as the anus.

GENERAL ANATOMY

The skin has an outer epidermis, consisting of a single layer of columnar epithelium, ciliated only within the oral hood and in parts of the atrium, and two layers of a fibrous cutis. The connective tissue is scanty, and consists of fibrillated ground substance with some cells. There is a thick muscular body-wall, of V-shaped segments separated by membranous myocommata, which fit into one another so that several are cut in a transverse section.

Within the body-wall lies a perivisceral cœlom, not divided by septa, but greatly complicated by the presence of the gill slits, which reduce it in the region of the pharynx to a number of canals in the primary gill bars (p. 302), a ventral canal called the sub-

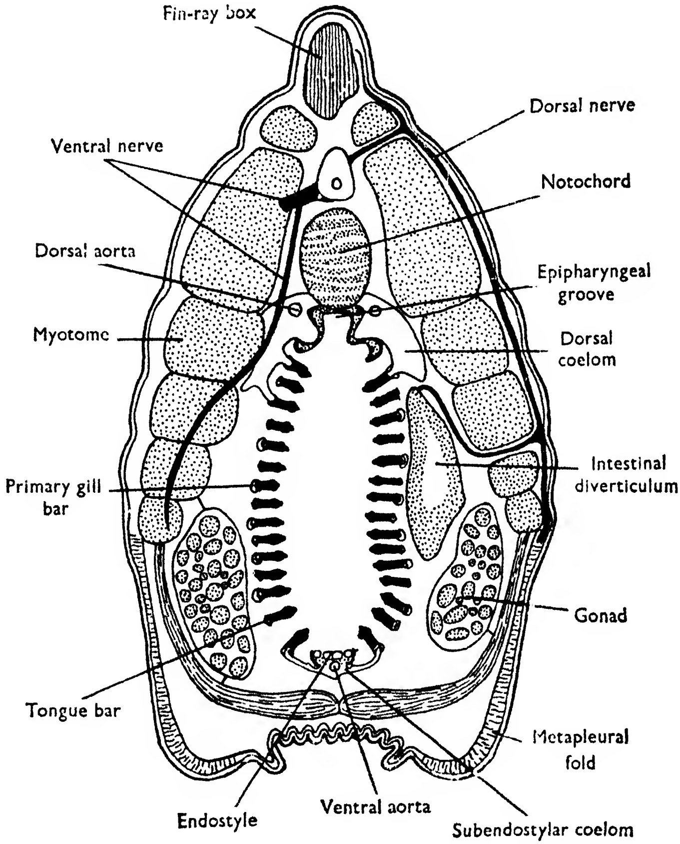


FIG. 20.3.—The lancelet. Transverse section through the the region of the pharynx.

endostylar cœlom, and on each side a longitudinal dorsal cœlom, all of these being in communication with one another. There are numerous cœlomic cavities, including those of the gonads. As in vertebrates, the dorsal body-wall is much thicker than the ventral. In it there lies a longitudinal, hollow central nervous system, comparable to that of vertebrates, but with no specialisation at the front end except for an expansion of the central canal. Below the central nervous system, but running the whole

length of the body to its extreme tip, lies an elastic rod, the notochord, which is bound to the nerve cord by a connective tissue sheath which surrounds them both. It consists of highly vacuolated cells and assists in swimming in two ways. The muscles of the two sides contract in a rhythmical and alternate manner, and the notochord, being incompressible, converts such unilateral contraction into a relatively sharp bending of the whole body. When the contraction of the muscles of one side is over, the elasticity of the notochord helps to produce a rapid flick back. There is no skeleton of bone or cartilage, but stiff rods of organic material support the gill bars and cirri, and the dorsal and ventral fins.

ALIMENTARY SYSTEM

The mouth leads into a buccal cavity or vestibule, which is nearly closed posteriorly by a partition called the velum. The

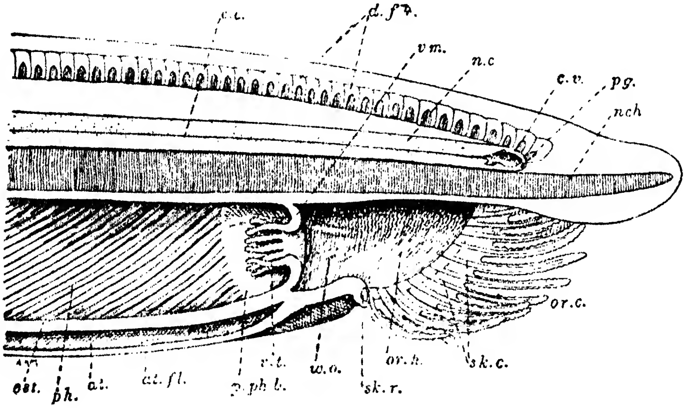


FIG. 20.4.—*Branchiostoma*. The forepart of the body cut in half longitudinally. *at.*, Atrium; *at.fl.*, atrial floor; *c.c.*, central canal of nerve cord; *c.v.*, cerebral vesicle; *d.f.r.*, dorsal fin rays; *est.*, endostyle; *n.c.*, nerve cord; *nch.*, notochord; *or.c.*, oral cirri; *or.h.*, oral hood; *p.ph.b.*, peripharyngeal band; *pg.*, anterior pigment spot; *ph.*, pharynx; *sk.c.*, skeleton of cirri; *sk.r.*, skeleton ring in oral hood; *v.t.*, velar tentacles; *vm.*, velum; *w.o.*, part of wheel organ.

opening in the centre of this leads into the pharynx, and is surrounded by about a dozen backwardly-projecting velar tentacles. Running round the buccal cavity just in front of the velum is a lobed structure called the wheel organ, which is covered with long cilia. Just in front of this there is a depression in the roof of the cavity known as Hatschek's pit. The hood can be contracted to close the mouth, and while the animal is feeding the oral cirri

are directed inwards and make a filter to exclude sand particles; the cilia in and around the mouth assist in producing an inwardly directed current, but there are sense cells both on the oral cirri and on the velum, and the chief function of these appears to be to test the water.

The pharynx runs for rather more than half the length of the body. Its wall, originally complete and containing part of the cœlom, is early in development pierced laterally by a number of visceral clefts or gill slits, and more of these are added as the animal grows, until there are nearly two hundred of them. They are oblique, the lower ends being posterior to the upper, so that

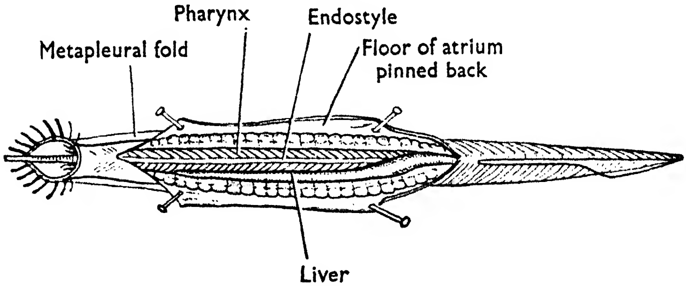


FIG. 20.5.—The lancelet. Ventral view, with the floor of the atrium cut open and pinned back. × 1.5.

several are cut in one transverse section. The first gill slits correspond to the myomeres, but later they become more numerous. The strips of body-wall left between the gill slits are called primary gill bars, and each contains a part of the cœlom and a skeletal rod. Each original gill slit is divided into two by the down-growth of a secondary or tongue bar, which contains a skeletal rod but no cœlomic space. Each slit is further subdivided by two or three horizontal bars or synapticulæ, also with skeletal rods. The inner (frontal) and anterior and posterior surfaces of the gill bars are covered with cilia; the last two groups of these, which project into the gill slit and are usually called lateral, although they are not on the sides of the body, beat outwards, and so maintain a current of water in at the mouth, down the pharynx, and out through the slits to the atrium and so to the exterior by the atriopore (Fig. 20.7). The frontal cilia beat upwards. On the floor of the pharynx lies the endostyle, which consists of four rows of ciliated cells alternating with four rows of mucus-secreting

cells. Food particles become entangled in the mucus, and the frontal cilia, which beat upwards, convey it to the roof of the pharynx, where there is a deep median epipharyngeal groove, with cilia which beat backwards. The feeding of the lancelet is thus very similar to that of the mussel (p. 274). Such feeding on small organic particles is called microphagy. A short distance in front of the atriopore the pharynx passes into the mid-gut, from which a large diverticulum runs forwards on the right side of the pharynx. This diverticulum is probably the chief digestive gland, since its cells are glandular and food does not enter it. All three classes of foodstuff are digested together in the mid-gut in an approximately neutral medium. The cilia of the posterior end of the mid-gut rotate the cord of mucus, and there is a short hind-gut which runs back to the anus. Absorption of food takes place chiefly in the hind-gut, but there is perhaps also some intracellular digestion in the mid-gut.

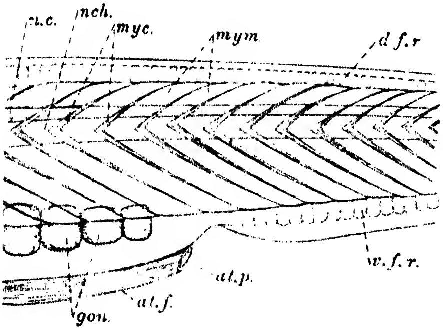


FIG. 20.6.—A view of the region around the atriopore of a specimen of *Branchiostoma* with the atrial floor expanded from the left side.

at.f., Atrial floor; *at.p.*, atriopore; *d.f.r.*, dorsal fin ray; *gon.*, gonads; *myc.*, myocommata; *mym.*, myomeres; *n.c.*, nerve cord; *nch.*, notochord; *v.f.r.*, ventral fin ray.

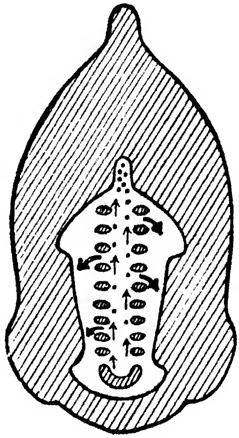


FIG. 20.7.—The outlines of a transverse section through the pharyngeal region of *Branchiostoma* with arrows to show the course of currents in the pharynx and atrium. Heavy arrows show the main current passing from pharynx to atrium, light arrows show the currents which transport to the epipharyngeal groove mucus containing the particles retained in the pharynx.

NEPHRIDIA

The lancelet possesses a series of nephridia, similar in their main structure to those of the more primitive annelids, lying between the wall of the atrium and the dorsal cœlomic canals. They correspond in number and position to the primary gill slits. Each is a bluntly branched tube (Figs. 20.8 and 20.9), with an opening below into the atrium, and dorsally a number of

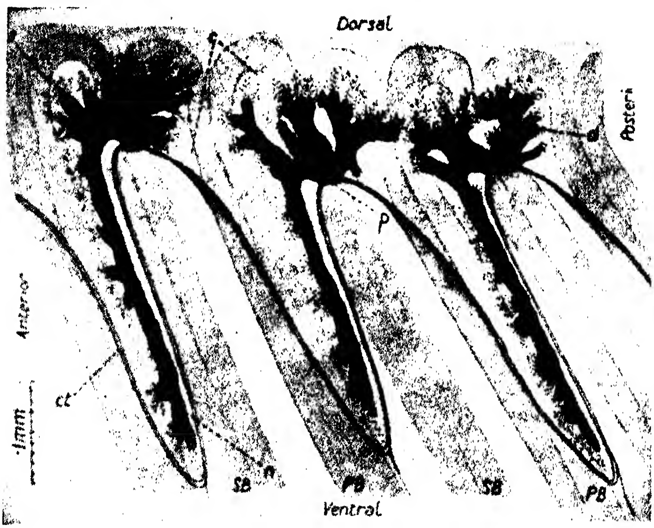


FIG. 20.8.—Three nephridia of *Branchiostoma lanceolatum* in situ, drawn with camera lucida from a stained preparation.—From Goodrich, *Quart. J. Micr. Sci.*, 1933. 75.

c., suprapharyngeal coelom; *ct.*, cut edge of atrial wall; *d.*, diverticulum of nephridial canal; *n.*, nephridium; *p.*, nephridiopore; *PB.*, primary gill bar; *s.*, solenocyte; *SB.*, secondary gill bar.

elongated flame cells or solenocytes, which project into the cœlom. The solenocyte is a single cell, with a nucleus in the knobbed end, and an intracellular duct into which hangs a single long flagellum. It is in close contact with special blood vessels, and as the flagellum seems to drive a current outwards to the atrium, it may be presumed to pass out excretory matter. The brown tubes, which are two dorsal diverticula of the posterior part of the atrium, may also be excretory.

VASCULAR SYSTEM

The blood is colourless and contains white corpuscles. The vascular system is closed. There is no heart, but the larger vessels are contractile and set up a circulation in which the blood flows forward ventrally and backwards dorsally (Fig. 20.10). A ventral or branchial aorta in the subendostylar cœlom gives off to each primary gill bar a vessel which divides to take part in the formation of a rather complicated branchial system in the primary and secondary bars and synapticulæ. On each side the branches of this system are gathered up into a series of vessels, which open into a longitudinal suprabranchial artery (or lateral dorsal aorta) beside the epibranchial groove, some of the blood passing through nephridial plexuses on the way. Behind the pharynx the suprabranchial arteries unite to form a dorsal aorta, which runs back under the notochord ; from the dorsal aortæ blood passes to lacunæ in the tissues, which take the place of capillaries. From the gut and body-wall, blood is collected by a subintestinal vein. This is for much of its course a plexus, but in front becomes a single vessel which runs to the liver and there breaks up again into a hepatic plexus. A hepatic vein, which is joined by a pair of vessels (ductus Cuvieri) from the body-wall, conveys the contents of this plexus to the ventral aorta.

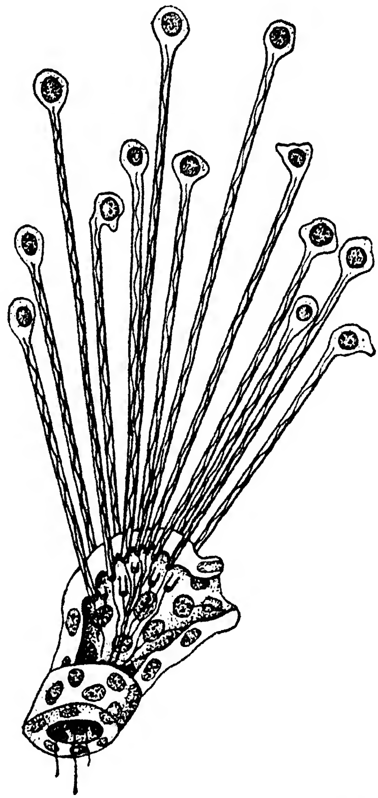


FIG. 20.9.—Solenocytes of *Branchiostoma*, showing the nuclei, long flagella, and the openings into the main excretory canal which leads to the atrium.—From Young, after Goodrich. Young, *The Life of Vertebrates*, 1950. Clarendon Press, Oxford.

The body contains a number of lymph spaces Some of these

(as those in the fins and certain spaces among the muscles) are of cœlomic origin. Others, such as the metapleural canals of the adult, may possibly be hæmocœlic. There is no evidence that the gill slits have any respiratory function, and at least when the animal is swimming, most of the oxygen is probably taken up through the skin.

NERVOUS SYSTEM AND SENSE ORGANS

The nerve cord is roughly triangular in transverse section, with a dorsal fissure, and flattened on its under side ; it ends abruptly in front at the level of the first myomere, and behind tapers to a point over the hind end of the notochord. The central

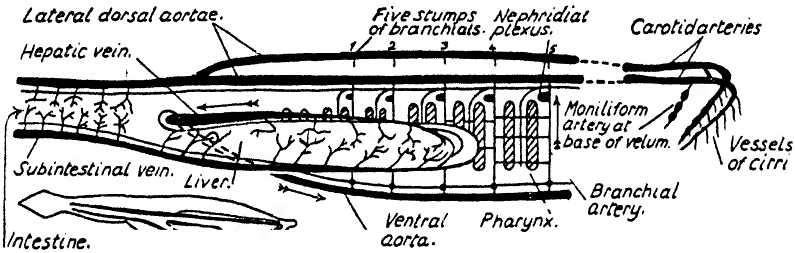


FIG. 20.10.—A diagram of the vascular system of *Branchiostoma*, from the right side, and slightly from above.

canal is lined by an epithelium, around it lie nerve cells, and the remainder of the cord is composed of non-medullated fibres. At the anterior end the canal widens out into a cerebral vesicle (Fig. 20.11), which in the larva communicates by a pore with a ciliated funnel known as the olfactory pit, on the dorsal surface of the left side of the body. In the adult this opening is lost, though the pit remains. A ciliated depression of the floor of the vesicle perhaps corresponds to the infundibulum of a vertebrate animal. The first pair of nerves arise from the lower side of the anterior end of the cord, the second pair from the dorsal surface behind the cerebral vesicle. These pairs are symmetrical. They are distributed to the epidermis of the structures round the mouth and are sensory in function. The remaining nerves are not symmetrical, but alternate with one another on the two sides, in correlation with the alternation of the myomeres. For each somite there is a dorsal nerve, which passes outside the myotome to the epidermis,

the non-segmented ventral muscles and the gut, and just in front of it a compound ventral nerve going direct to the myotome. These possibly correspond to the dorsal and ventral roots of the spinal nerves of a mammal. The ventral nerves are motor, and the dorsal nerves mixed, but the latter have their cell bodies at the periphery of the body like an invertebrate (Fig. 13.11), not, like a vertebrate, in ganglia. The sense organs are few and simple. Supposed tactile cells bearing short, stiff processes are scattered among the ordinary ectoderm cells, especially at the front end of the body and around the mouth, and the animal responds to touch by swimming backwards or forwards as the front or hind end is stimulated. Possible chemoreceptors are the olfactory pit and cells of the oral cirri. The mass of pigment which lies in the front wall of the cerebral vesicle probably protects that part of the cord from light; more posteriorly in the lower part of the nerve cord are cells which appear to be sensitive to light.

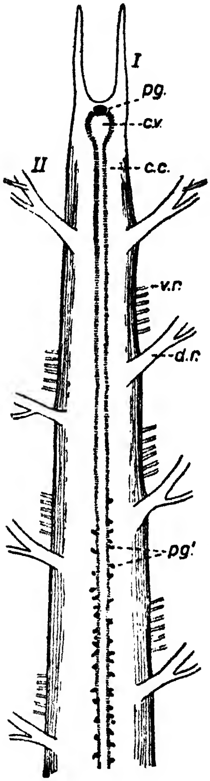


FIG. 20.11.—The front part of the nerve cord of *Branchiostoma*, seen from above.

c.c., Central canal; *c.v.*, cerebral vesicle; *pg.*, anterior pigment spot; *pg'.*, pigment spots in the floor of the cord; *v.r.*, ventral root; *d.r.*, dorsal root; *I*, *II*, first two pairs of nerves.

REPRODUCTIVE ORGANS

The sexes of the lancelet are separate, but show no differences save in the nature of the gonads. These are cubical bodies, twenty-six on each side, situated in the wall of the atrium, into which they shed their products by rupture of their walls. Each corresponds to one of the myomeres and consists of a closed cœlomic sac, whose cavity is known as the gonocœle and on whose wall the gametes arise, though they are actually derived, by a rather complicated process, from the epithelium of the embryonic cœlom of the myomere behind that in which they lie. The egg is minute, but contains yolk granules. The gametes are shed in spring, and are carried out by the current through the atriopore

and fertilisation takes place in the water. The further development is described in Chapter 28.

CHORDATA

The lancelet is a member of the phylum Chordata, and possesses most of the features of the group in an almost diagrammatic form, uncomplicated by the specialisations and complications of the higher types. The chordates resemble the annelids in being segmented cœlomate Metazoa, but they differ from all other phyla in possessing the following four structures : a dorsal notochord ; a nerve cord which is hollow, single and dorsal ; visceral or gill clefts opening from the pharynx to the exterior ; and a post-anal tail containing no viscera ; further, the blood flows forward in the ventral vessel. All these we have seen in the lancelet, but in some of the other primitive chordates one or other of the characteristics may be missing, and in the higher forms they tend to be lost or obscured in the adult. Apart from possession of some of the fundamental characters of the phylum, the primitive groups have little resemblance to each other, and are therefore most conveniently arranged as subphyla. Such a division makes four sections of the chordates, thus :

SUBPHYLUM I—HEMICHORDATA

These are well described by their name, for they are only half chordates, or less. One class, the Enteropneusta, represented by *Balanoglossus*, a marine worm-like animal, has gill slits, a partially hollow nerve cord, and a somewhat doubtful notochord, while the other class, the Pterobranchia, represented by the colonial *Rhabdopleura*, have only the doubtful notochord and, in some genera, a single gill slit. They are interesting only as clues in speculation on the origin of the phylum.

SUBPHYLUM II—CEPHALOCHORDATA

Branchiostoma adequately illustrates the structure of the group, which contains only one other genus. The notochord reaching to the extreme anterior end, the numerous gill slits, and the atrium, may be taken as characteristic.

SUBPHYLUM III—UROCHORDATA OR TUNICATA

The only chordate feature possessed by most adults is the gill slits, but in the larva there is a short notochord in the tail. The nervous system is reduced to a ganglion, and the direction of flow of blood periodically reverses. The adult is almost completely surrounded by a case made of tunicin, a substance very similar to cellulose in composition. Many adults are sessile, such as *Ciona* on British coasts, and some are colonial, but the larvæ are pelagic and tadpole-like.

These three subphyla are spoken of collectively as protochordates. There remains :

SUBPHYLUM IV—VERTEBRATA

This is dealt with more fully in later chapters.

21

THE DOGFISH

VARIOUS species of the small sharks known as dogfish are found in British waters. One of the commonest in southern seas is the lesser spotted dogfish or rough hound, *Scyllium canicula* (=*Scyliorhinus caniculus*), but in the north this is replaced by the larger spiny or piked dogfish, *Acanthias vulgaris* (=*Squalus acanthias*) which is found also in American seas. The following description applies primarily to the former, but the chief differences of *Acanthias* are noted. Like other dogfish, they justify their name by travelling in packs and hunting by smell. They live usually near the sea bottom, and feed largely upon crabs, hermit crabs, and other crustaceans, though they also devour shell-fish, or small fishes, and will indeed take most kinds of animal food, dead or alive. They are very voracious and are a nuisance to fishermen by taking the bait meant for their betters. The flesh, though coarse, is used for food.

EXTERNAL FEATURES

The length of a well-grown rough hound is about two feet. Its slender body, well shaped for passage through the water, tapers from before backwards, and, though it shows no sudden differences in size, there may be recognised in it a head, a trunk, and a tail, the hinder limit of the first being marked roughly by the hindmost gill slit (see below), and that of the trunk by the vent. The head is flat, and has a blunt-pointed snout, a wide, crescentic mouth on the lower side, a pair of round nostrils in front of the mouth and connected with it by oronasal grooves, and at the sides two slit-like eyes. Immediately behind each eye is a small, round opening, the spiracle, while farther back and more towards the ventral side is a row of slits which are the gill slits or gill clefts. The spiracle and the gill clefts open internally into the pharynx. Behind the head the body gradually changes its shape, becoming flattened from side to side instead of from above downwards. The vent or opening of the cloaca lies in a deep longitudinal groove of the belly, just before the middle of the body. Into the same groove there opens at each side one of the abdominal pores, which lead from the body cavity. There

are two pairs of fins and four unpaired fins. The fore or pectoral fins, corresponding to the arms of man, are a pair of flat, triangular organs attached by one angle to the sides of the ventral surface not far behind the head. The hinder or pelvic fins are smaller and narrower structures of somewhat the same shape, attached one on each side of the middle line of the belly in front of the vent. In the male, their inner edges are fused and there projects backwards from the under surface of each a rod, grooved along its inner side, known as a clasper or pelvic process. The unpaired fins are median structures in the tail. Two, known as the anterior and posterior dorsal fins, are on the back, one, the ventral fin, is on the under side, and another, the caudal fin, surrounds the end of the tail. This fin has two lobes of unequal size, and the skeleton of the tail is turned upwards and passes into the larger upper lobe. This type of asymmetrical tail is called heterocercal. *Acanthias* has a long spine, from which it gets its name, in front of each dorsal fin.

GENERAL INTERNAL FEATURES

Certain generalisations which we have made in the course of the previous chapters enable us to state in a few words a good deal of information about the anatomy of the dogfish. The dogfish is metazoan, triploblastic, cœlomate and bilaterally symmetrical. It is also segmented (p. 191), though the primary segmentation is best seen in the early stages of development and is represented in the adult only by the arrangement of the muscles of the body-wall, the segmentation which is found in the backbone and nervous system arising later. It is chordate (p. 308), and lastly it is a backboned or vertebrate animal. This means that it possesses a jointed internal skeleton, and some other features which we shall discuss later.

SKIN

Upon the back and sides of the rough hound the skin is of a grey-brown colour with small spots of darker brown ; upon the belly it is whitish. It changes colour slowly to match its background, control being by the pituitary gland (p. 336). The outer part of the skin is largely composed of the protein keratin, and although it feels smooth to the hand if it be stroked from head to

tail, it is rough if it be stroked in the opposite direction. This is due to the presence of scales, which are not flat like those of most fishes, but bear minute spines directed backwards (Fig. 21.1). Each consists of a calcified basal plate embedded in the dermis, and a spine which is composed of dentine covered with a very hard substance called enamel. A pulp cavity, containing highly vascular connective tissue, passes through the base into the spine. The structure is thus that of a tooth (p. 360) and scales of this

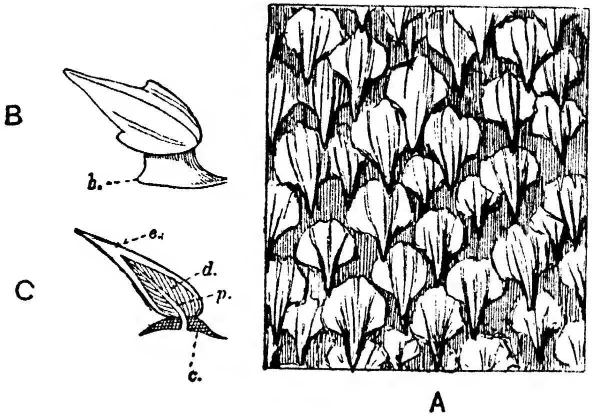


FIG. 21.1.—Placoid scales.

A, A portion of the skin of the rough hound as seen under a hand lens ; *B*, a single scale removed from the skin ; *C*, the same in section (diagrammatic).
b., Base of the scale ; *c*., the same in section ; *d*., dentine ; *e*., enamel ; *p*., pulp cavity.

type are called placoid. Teeth must be looked on from the evolutionary point of view as modified placoid scales. The teeth of the dogfish, which differ from the scales only in size, form an intermediate link.

MUSCLES AND MOVEMENTS

In the body-wall (Fig. 27.18) the muscles are for the most part segmentally arranged, each muscle-segment being known as a myomere (Fig. 21.2). The myomeres do not lie straight, but each is bent five times, so that it runs a zigzag course from the middle of the back to that of the belly. In the muscles of the head, throat, and fins the segmental arrangement is not apparent. The myomeres are separated by partitions of connective tissue (myocommata, singular myocomma), between which their fibres

run longitudinally. When the fish is swimming, waves of curvature are produced by alternate contraction of the muscles of the two sides (especially powerful in the tail, which is more than half the

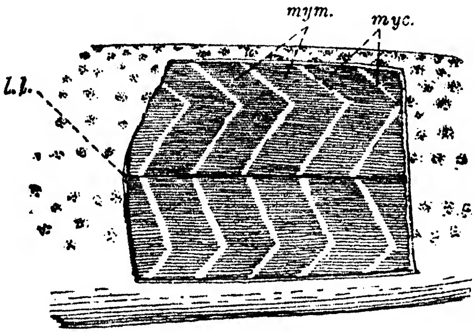


FIG. 21.2.—The hinder part of the trunk of a dogfish seen from the left side, with a piece of the skin removed.

l.l., Tube of the lateral line ; *myc.*, myocommata or septa of connective tissue ; *mym.*, myomeres.

length of the body). These waves travel from head to tail, and the leading, caudally-facing, surface is always directed obliquely backwards except when it is at its extreme displacement (frames

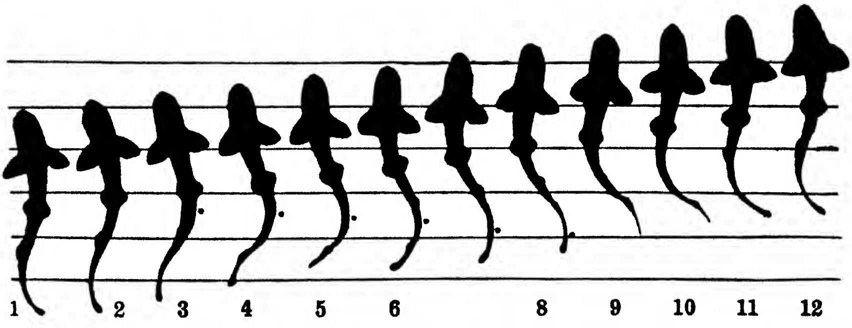


FIG. 21.3.—Successive positions of a swimming dogfish at intervals of 0.1 sec. The lines are 3 in. apart. The passage of a wave is marked by dots.—From Young, *The Life of Vertebrates*, 1950. Clarendon Press, Oxford. After Gray.

3 and 8 in Fig. 21.3). Since the lateral components of the force which the moving tail exerts on the water are alternated and cancel each other out, the resultant is a force directed backwards. The equal and opposite force exerted, in accordance with Newton's first law, by the water on the fish, drives the fish forward. The tail fin (though in this respect less important than that of most fishes)

adds to the propellant surface which is applied to the water when a wave reaches the end of the body. To produce a turn, a strong contraction is sent down one side and turns the head to that side. The tail, owing to the resistance offered by its fin, stands firm as a fulcrum for the head-turn ; afterwards it is swung into line with the head. The unpaired fins act like the keel of a boat in reducing rolling and yawing, while the heterocercal tail, acting in conjunction with the pectoral fins acting as elevators, enables the fish to alter its level in the water.

SKELETON : GENERAL FEATURES

The endoskeleton of the dogfish corresponds to that of the rabbit in its main outlines, but differs from it in some important respects. (1) It is wholly cartilaginous (p. 520), though in places the cartilage is calcified. (2) The axial skeleton (pp. 314–8) is traversed longitudinally below the central nervous system by a peculiar rod, the notochord, which consists of large vacuolated cells with stout walls. (3) There are no structures which represent any part of the breast bone. (4) In correspondence with the difference in form of the limbs there are large differences between their skeletons.

VERTEBRAL COLUMN

The main axial skeleton consists of about 130 vertebræ (p. 570). In each of these the main portion or centrum, has grown round the embryonic notochord and has constricted it in the middle, so that the isolated vertebra is a biconcave cartilaginous disc, with a hole in the middle through which the notochord passed. On each side the centrum bears a pair of ventrilateral processes (Figs. 21.4, 21.11) which are often called transverse processes, though they do not correspond with the transverse processes of the rabbit, which belong to the neural arches. In the trunk region these are directed outwards and bear short ribs, which lie beneath the muscles of the back ; in the hinder part of the body the processes are directed downwards and meet to form hæmal arches, which enclose a hæmal canal, in which lie the caudal artery and vein. Towards the hinder end of the tail the ventrilateral processes fuse at their ends and bear a median hæmal spine. Between the neural arches of successive vertebræ are wide gaps which are closed by intercalary pieces. A series of flat median pieces of

cartilage, the supradorsals, twice as numerous as the vertebræ, fill the gaps between the tops of the neural arches and intercalary pieces, and roof in the vertebral canal.

THE SKULL

The skull is built on the usual vertebrate plan, with a dorsal part in association with the brain, and a ventral part in association with the gill slits. The dorsal part, to which the term skull

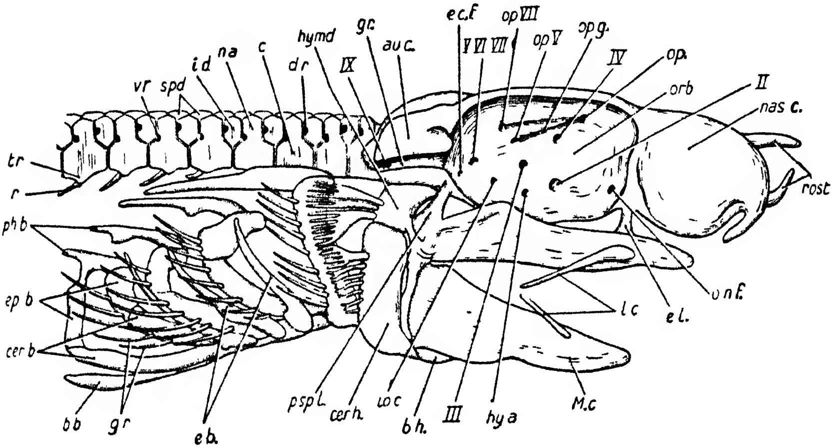


FIG. 214 Skull and branchial arches of the dogfish (*Scyliorhinus*).—From Young, *The Life of Vertebrates*, 1950 Clarendon Press, Oxford

au c Auditory capsule, *b b*, basibranchial, *b h*, basihyal, *c*, centrum, *cer b*, ceratobranchial, *cer h*, ceratohyal, *d r*, foramen for dorsal root, *e b*, extrabranchial, *e.c f*, external carotid foramen, *e l*, ethmoid ligament *ep b* epibranchial *gr*, groove for anterior cardinal sinus, *g r*, gill ray, *hy a*, foramen for hyoid artery, *hymd*, hyomandibular, *i d*, interdorsal, *io c*, interorbital canal, *l c*, labial cartilage, *M c*, Meckel's cartilage, *na*, neural arch, *nas c.*, nasal capsule, *o n f*, orbitonasal foramen; *op.*, foramen for ophthalmic nerve; *op.g.*, groove for ophthalmic branch of fifth nerve; *op.V.*, foramen for the same; *op.VII.*, foramen for ophthalmic branch of seventh nerve; *orb.*, orbit; *ph.b.*, pharyngobranchial; *p.sp.l.*, prespiracular ligament; *r.*, rib; *rost.*, rostral cartilage; *spd.*, supradorsal; *tr.*, transverse process; *v.r.*, foramen for ventral root; *II–IX*, foramina for cranial nerves.

is sometimes restricted, consists of the brain-box or cranium, and attached to this a pair of anterior olfactory capsules and a pair of posterior auditory capsules. The projections of the cranium above and below the orbits are called supraorbital and suborbital ridges. In the anterior part of the roof of the cranium there is a large gap; such an area of incompleteness in the cartilage of the cranium is called a fontanelle, and this one, from its position, is the anterior fontanelle; others, in different positions, occur in other animals. Through the fontanelle the brain may be seen. Posteriorly the cranium has two knobs, the occipital condyles,

which fit into hollows on the first vertebræ. The nasal capsules, thinner than the rest of the skull, are continuous with the cranium, and are roughly spherical in shape. Their ventral surfaces are incomplete. Running vertically between them is the internasal septum or mesethmoid cartilage. Three slender rods, one from each capsule and one from the mesethmoid, project forwards and are known collectively as the rostrum. The auditory capsules are also continuous with the cranium, and except for a pair of small openings on the dorsal surface, completely enclose the ears; ridges on the capsules mark the positions of the semicircular canals (p. 342). Between the auditory capsules is the foramen magnum, through which the spinal cord passes into the brain, and just below this the notochord may be seen going into the floor of the cranium, in which it runs about half-way along. There are several other openings, called foramina (singular foramen) through which nerves or blood vessels pass into or out of the cranium; the more important of them are shown in Figs. 21.4 and 21.5.

The visceral part of the skull consists of a series of half-hoops of cartilage on each side, developed in the tissue between the gill slits and behind the last gill slits, so that they correspond in position to the gill bars of *Branchiostoma*. Each pair of half-hoops forms a nearly complete hoop, which circles the body except on the dorsal side, where there is a gap. The first hoop, called the mandibular arch, forms the skeleton of the jaws; it has two parts; above the mouth is the palatopterygoquadrate bar, which is hung from the auditory capsule by a postspiracular ligament and from the cranium by an ethmopalatine ligament, and which is joined to its fellow in front by another ligament; below the mouth is Meckel's cartilage, articulating with (that is, resting against and able to move relatively to) the palatopterygoquadrate behind and joined to its fellow by ligament in front. At the junction of the two cartilages ligaments join them to the hyomandibula (see below); this is their chief connection with the dorsal part of the skull. The arrangement by which the upper jaw is slung from the skull by the hyomandibular is called a hyostylic jaw suspension. This and other types of suspension are discussed on pages 588–90. Each of the remaining half-hoops consists of a number of pieces of cartilage; the general plan is for there to be five of these, which are called, from above downwards, pharyngo-, epi-, cerato-, hypo- and basi-branchial cartilages, the

last being a median piece, common to the two sides. Behind the spiracle, which is considered to be a modified gill slit, lies the

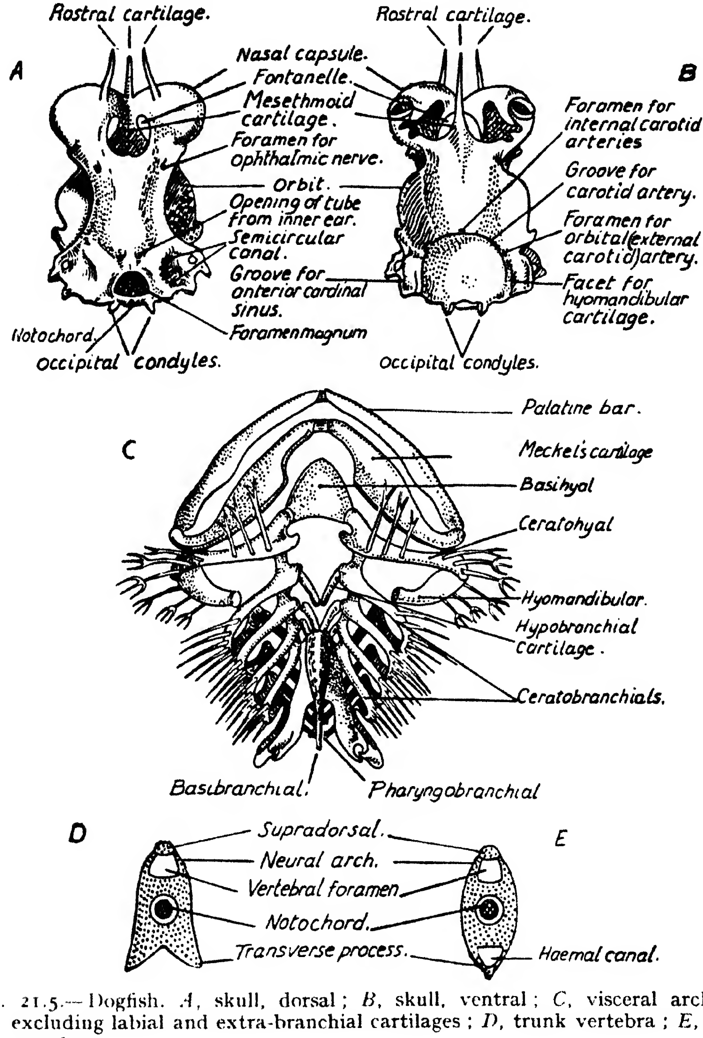


FIG. 21.5.—Dogfish. *A*, skull, dorsal; *B*, skull, ventral; *C*, visceral arches, excluding labial and extra-branchial cartilages; *D*, trunk vertebra; *E*, tail vertebra.

hyoid arch, which has only three parts. The uppermost, called the hyomandibula, or hyomandibular cartilage, is really the epihyal; it is, as we have already seen, attached to the jaws, and above, it is firmly held by ligaments to the auditory capsule.

Below it, the ceratohyal passes forwards and joins the basihyal, which lies in the floor of the mouth. *Scyllium* and *Acanthias* have five pairs of gill slits, so that there are five more hoops, each called a branchial arch, and the whole is sometimes called the branchial basket. (Other sharks have more gill slits and so more arches, one behind each.) The first hypobranchial joins the basihyal; the second hypobranchial meets its fellow and has no basi-element; the third and fourth hypobranchials join a single basibranchial; the fifth hypobranchial is missing, but the fifth ceratobranchial joins the basibranchial. The epi- and cerato-branchials are distinguished from the other elements by bearing along their hinder borders gill rays which support the gills. The two paired elements of the hyoid also bear rays, showing their homology with the epi- and cerato-elements.

Outside the upper and lower jaws lie a pair of labial cartilages, and along the outer sides of the second, third, and fourth cerato-branchials are extrabranchials.

FINS

The median fins are supported by a skeleton consisting of several series of rays. The series nearest the body are cartilaginous rods known as basalia and are attached to the neural and hæmal spines. They are succeeded by a similar series known as cartilaginous rays or radialia, and these by two rows of small, polygonal plates of cartilage which are overlapped at the sides by a double series of horny rays or dermotrichia that project beyond them. The dermotrichia, which belong to the dermis, are fine fibres composed of the same substance (elastin) as the elastic fibres of connective tissue (p. 517). In the caudal fin the cartilaginous rays are not distinct from the supradorsals and hæmal spines.

The limbs are anchored into the body by girdles which correspond to those of man, though neither is attached to the backbone. The pectoral or shoulder girdle (Fig. 21.6) consists of a single nearly complete hoop of cartilage open on the dorsal aspect; it is formed in development from two cartilages, the scapulocoracoids, the ventral coracoid portions of which meet and fuse in the middle line. At about the middle of the posterior surface of each scapulocoracoid is a hollow, the glenoid facet, with which the skeleton of the fin articulates; this facet marks also the division into ventral coracoid and dorsal scapular regions. The coracoid

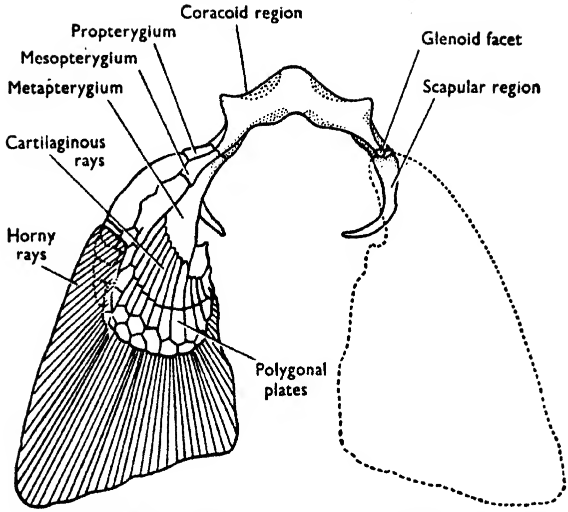


FIG. 21.6.—*Scyllium canicula.* Ventral view of the skeleton of the pectoral girdle and pectoral fin. The left fin is shown in outline only. × 0.5.

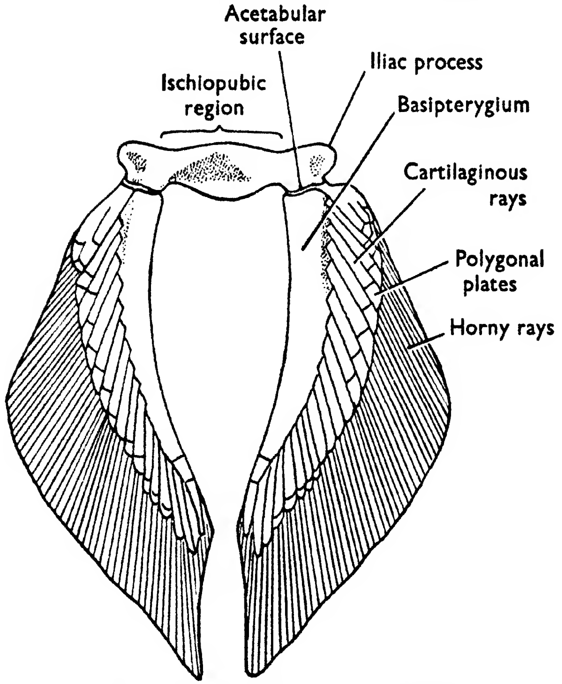


FIG. 21.7.—*Scyllium canicula.* Ventral view of the skeleton of pelvic girdle and fins of female. × 0.5.

is broad and flat, and supports the floor of the pericardium ; the scapular part is a curved rod. The pelvic or hip girdle (Fig. 21.7) is a stout straight bar running transversely just in front of the anus ; it is formed by the fusion of right and left ischiopubic cartilages, each of which has a knob, the iliac process, at its outer end. The fin articulates with an acetabular facet on the hinder border at the base of the iliac process.

The skeleton of the paired fins is similar to that of the unpaired fins, that is, there are basalia, radialia, polygonal plates and a double series of dermotrichia. The pectoral fin has three basals, called pro-, meso-, and metapterygia, of which the first is anterior and smallest, the last posterior and largest; all these articulate with the girdle, but they are not movable on each other ; the pro- and mesopterygia have one radial each, the metapterygium has several. In the pelvic fin there is a single basal, the basipterygium, which bears several radials. In the male there is also a long piece of cartilage supporting the clasper.

CŒLOM AND ALIMENTARY SYSTEM

The perivisceral cavity (cœlom) is divided into two parts, the small pericardial cavity just in front of the pectoral fins, and the large peritoneal cavity behind it, between the two pairs of fins. The

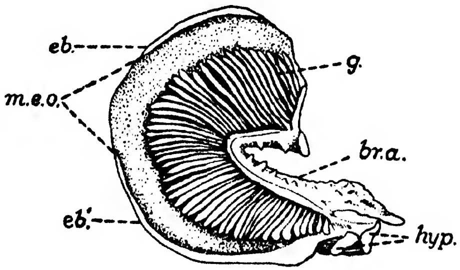


FIG. 21.8.—The hinder wall of a gill pouch of the dogfish.

br.a., Branchial arch, flexed because the pharynx floor is raised ; *eb.*, *eb'.*, extrabranchials ; *g.*, gill ; *hyp.* hypobranchials in section ; *m.e.o.*, margin of external opening.

two cavities are divided by a membranous septum, but a narrow passage, the pericardio-peritoneal canal, leads from one to the other below the œsophagus, and can be found in dissection by probing with a seeker behind and above the heart. From the

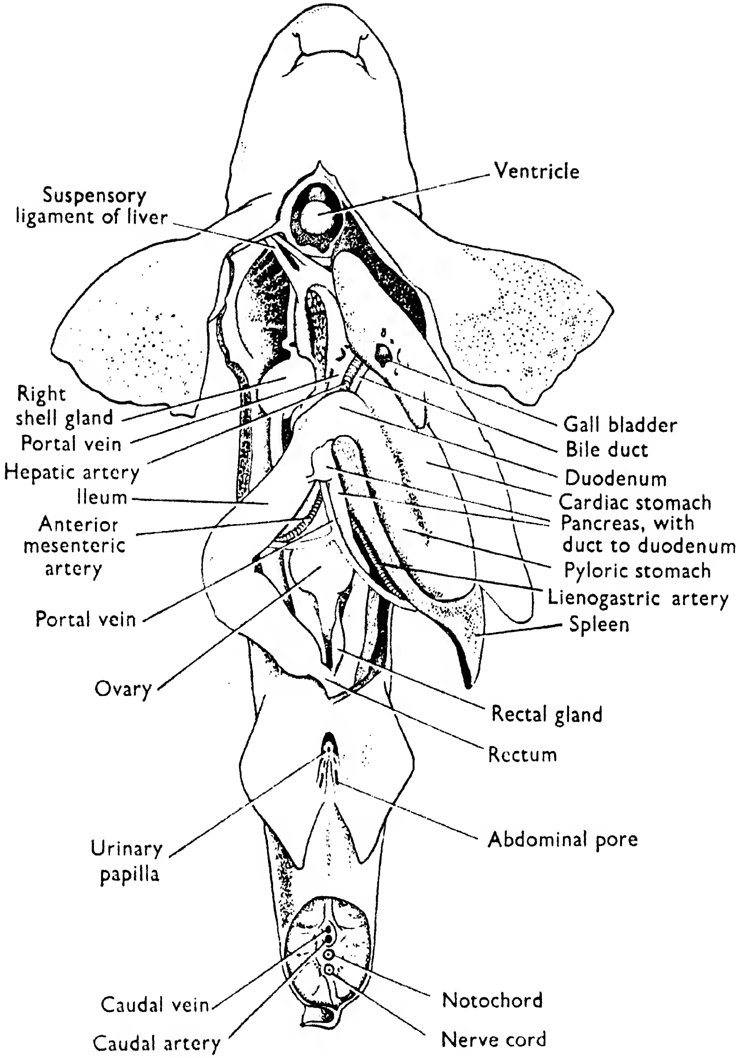


FIG. 21.9.—*Scyllium canicula*. A female with the abdominal and pericardial cavities opened from the ventral surface, the viscera somewhat displaced, and the right lobe of the liver cut away. × 0.5.

peritoneal cavity the two small abdominal pores lead to the exterior, one on either side of the vent. The gape of the mouth is edged with several rows of teeth, which as we have seen, are simply enlarged scales ; their function is only to hold the food, not to cut or chew it. They lie in a part of the skin which passes over the jaw and is tucked into a groove within it and are not in any way attached to the skeleton of the jaw. Teeth formed in the groove are continually being carried forward over the edge of the jaw by the growth of the skin, so that as they wear away they are replaced by new ones, a type of dentition called polyphyodont. The pharynx is only distinguished from the buccal cavity by possessing the inner openings of the spiracle and gill clefts. These are placed between the arches of the visceral skeleton, the first gill cleft lying between the hyoid and first branchial arches. The clefts slant backwards so that the outer opening of each is at some distance behind the inner. The spaces between inner and outer openings, known as gill pouches, are considerably taller than the openings themselves. On each wall of each pouch except the last lie a number of folds which constitute a gill or hemibranch (Fig. 21.8). This is highly vascular, and in fresh specimens has consequently a bright red colour. The last pouch has a gill on the anterior side only. The spiracle is a small cleft of the same series as the gill clefts, and bears on its front side a vestige of a gill, known as a pseudobranch. The bars of body-wall between the mouth and spiracle, between the spiracle and first gill slit, and between the gill slits, are known as visceral arches and have the same names as the skeletal arches which they contain (p. 316). Each contains also arteries and nerves. The movements of the visceral arches, which carry out the processes of feeding and, as we shall see, of breathing, are brought about by muscles which run between the cartilages of the arches and the coracoid region of the shoulder girdle. The pharynx passes into the narrower œsophagus which lies in the peritoneal cavity and soon merges into the stomach (Fig. 21.9). The cardiac portion of this is an elongated sac ; near its hinder end on the right side the narrow tubular pyloric division arises and runs forwards beside the cardiac. A slight constriction at the anterior end of this marks the presence of the pyloric sphincter which divides it from the intestine. The first part of this is a short narrowish duodenum which receives the ducts of the liver and pancreas. Behind this is the ileum, which is long and wide and directed backwards,

and has its internal surface increased by a spiral fold of the mucous membrane known as the spiral valve (Fig. 21.10) ; its hinder end opens into a narrow rectum without a spiral valve. This in turn ends in a wider cloaca, which receives the urinary and genital ducts and opens by the vent.

The liver is a very large organ, consisting of long right and left lobes united in front and slung by the suspensory ligament from the anterior wall of the peritoneal cavity. The gall-bladder is embedded in the front part of the left lobe of the liver, but usually a part of it shows upon the surface. From it the bile duct runs backwards to open into the intestine, lying in the membrane or omentum which carries the hepatic artery and portal vein. The pancreas lies between the stomach and intestine ; it is long and narrow and has in front a rounded ventral lobe, from which its duct passes to the ventral side of the intestine. The rectal gland is a small, cylindrical structure which opens into the dorsal side of the rectum by a duct. The spleen, which has no functional connection with the alimentary canal, is a triangular body attached by a membrane to the hinder end of the stomach, with a prolongation running forward along the right side of the pyloric division.

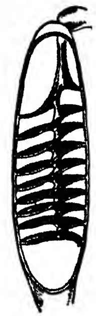


FIG. 21.10.—Diagram of spiral valve. —After T. J. Parker.

Digestion follows the same general course as in mammals (p. 440) ; the food remains in the stomach, which is even more acid than in man, for two or three days or even longer.

RESPIRATION

The hemibranchs meet across the gill pouch and divide it into two chambers. When the floor of the pharynx is lowered water is drawn in through the mouth and spiracles, while the flexible front edge of each gill slit is caused, by the lower pressure within, to flap back so as to prevent the entry of water that way. When the floor is raised the lips prevent the escape of water through the mouth, contraction of the œsophagus keeps that also closed, and the water, being under pressure, opens the clefts and passes out

through the gills. Water is also sucked into the outer part of the gill chamber by contraction of muscles in its walls; when the chamber contracts, back flow of water to the pharynx is prevented by the high resistance of the gills. Through the thin membrane which is all that separates the blood in the gills from the water, the gases of respiration are exchanged.

BLOOD VESSELS: HEART

The heart of a dogfish lies in the pericardium at the level of the last gill cleft. It is a median structure with muscular walls, and consists essentially of an irregular tube, bent twice like an S

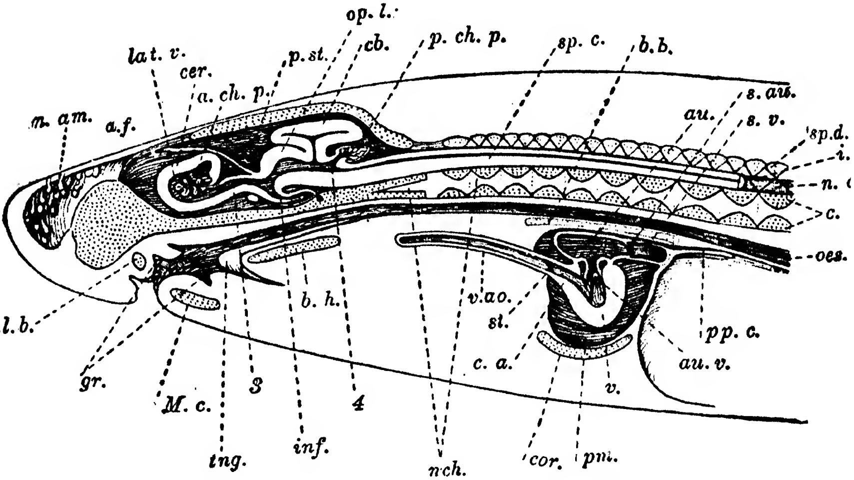


FIG. 21.11.—A semi-diagrammatic drawing of a longitudinal section through a dogfish, passing slightly to the right of the middle line.

a.ch.p., Anterior choroid plexus; *a.f.*, anterior fontanelle; *au.*, auricle; *au.v.*, auriculo-ventricular opening and valve; *b.b.*, basibranchial cartilage; *b.h.*, basihyal cartilage; *c.*, centrum; *c.a.*, conus arteriosus; *cb.*, cerebellum; *cer.*, cerebrum; *cor.*, coracoid region of the pectoral girdle; *gr.*, grooves in which the teeth are formed; *i.p.*, intercalary plate; *inf.*, infundibulum; *lat.v.*, lateral ventricle; *M.c.*, Meckel's cartilage; *n.a.*, neural arch; *n.am.*, ampullary sense organs; *nch.*, notochord; *oes.*, œsophagus; *op.l.*, optic lobe; *p.ch.p.*, posterior choroid plexus; *p.st.*, pineal stalk; *pal.b.*, palatine bar; *p.m.*, pericardium; *pp.c.*, pericardio-peritoneal canal; *s.au.*, sinu-auricular opening; *s.v.*, sinus venosus; *sp.c.*, spinal cord; *sp.d.*, supradorsal cartilage; *st.*, semilunar valves; *tng.*, tongue; *v.*, ventricle; *v.ao.*, ventral aorta; 3, third ventricle; 4, fourth ventricle.

(Fig. 21.11) and composed of four successive chambers. The hindermost chamber is the thin-walled sinus venosus, which is triangular as seen from below, and lies with its base against the hinder wall of the pericardium. In front of it comes the thicker-walled auricle. This is also triangular, with its apex forwards, and has its hinder angles widened into pouches. The S then curves downwards, as

the very thick-walled, conical ventricle, which lies below and somewhat behind the auricle. From it the narrow conus arteriosus passes forwards through the front wall of the pericardium to become the ventral aorta, which is merely the foremost part of the single vessel whose thickening and twisting produces the heart behind. Thus the heart, or contractile blood vessel, of the dogfish, like that of all other vertebrate animals, is ventral in position, whereas the principal contractile vessel of an invertebrate is generally dorsal. The heart contracts from behind forwards and drives blood into the ventral aorta, reflux being prevented by valves at the opening of the sinus into the auricle and again at the auriculo-ventricular opening, and by two rings of semilunar or watch-pocket valves in the conus. All the blood which enters the heart comes from active tissues, so that only deoxygenated blood is pumped to the gills.

ARTERIES

The ventral aorta runs forward below the pharynx and divides just above the thyroid gland. Each branch almost immediately divides into the first and second afferent branchial arteries. Between them and the heart the aorta gives off three more pairs, making five in all. The afferent branchial arteries, together with the aorta, form the ventral arterial system. From the afferent branchial arteries the blood passes into the capillaries of the gills, where it is oxygenated and gathered up into efferent branchial arteries. These form a complete loop round each of the first four clefts, the loops being joined fore and aft by short horizontal vessels at about the middle of their lengths. The last cleft, having no gill on its hinder side, has an efferent vessel on its front side only, and all the blood of this vessel passes by the horizontal vessel into that of the gill in front. From the dorsal end of each of the complete loops arises a vessel known as an epibranchial artery, which runs backwards and inwards on the roof of the pharynx to join the median dorsal aorta opposite to its fellow of the other side. From the dorsal end of the first efferent branchial artery, just outside the origin of the first epibranchial artery, arises the root of the carotid artery. This is often called the 'common carotid artery', but it does not correspond to the vessel of that name in the higher vertebrates.

It runs forwards and inwards under the skull and is presently joined by a small branch from the dorsal aorta (see below), after

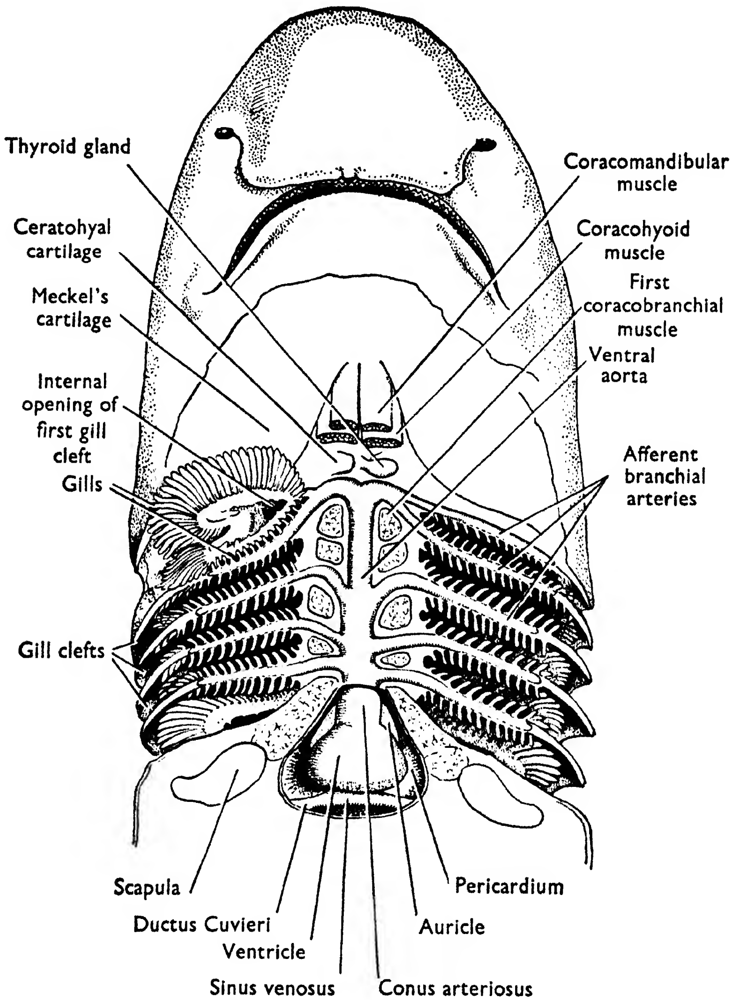


FIG. 21.12.—*Scyllium canicula*. The head dissected from the ventral surface to show the heart and afferent branchial arteries. × 1.

which it becomes the carotid (internal carotid) artery. Behind the orbit it gives off forward an orbital branch which immediately passes through the opening in the floor of the skull and runs

forwards along the floor of the orbit to supply the upper jaw and the snout. (This branch is often called the external carotid artery but does not correspond to the external carotid

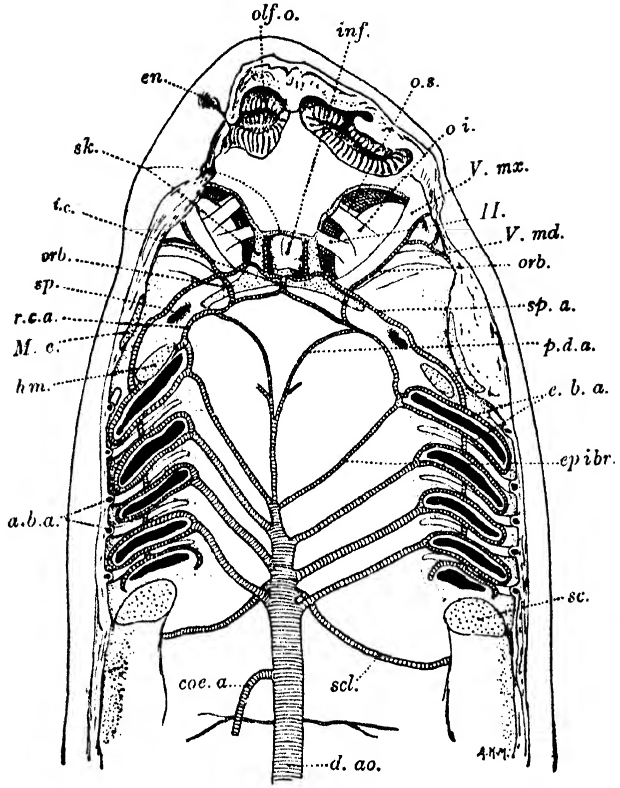


FIG. 21.13.—The forepart of a dogfish, dissected from the ventral side, to show the dorsal arterial system, the olfactory organs, and certain structures in the orbits. The middle part of the floor of the mouth has been removed.

a.b.a, Afferent branchial arteries; *coe.a.*, cœliac artery; *d.ao.*, dorsal aorta; *e.b.a.*, efferent branchial arteries; *en.*, nostril; *epibr.*, epibranchial artery; *h.m.*, hyomandibular cartilage; *i.c.*, internal carotid foramen; *inf.*, infundibulum; *M.c.*, Meckel's cartilage in lower jaw; *o.i.*, inferior oblique muscle; *o.s.*, superior oblique muscle; *olf.o.*, olfactory organ; *orb.*, orbital or 'external carotid'; *p.d.a.*, prolongation of aorta; *r.c.a.*, carotid root; *sc.*, scapula; *scl.*, subclavian artery; *sk.*, skull; *sp.*, spiracle; *sp.a.*, spiracular artery; *V.md.*, *V.mx*, mandibular and maxillary branches of fifth nerve; *II.*, optic nerve.

of the rabbit). The carotid artery continues its course in the carotid groove, towards the middle line, where it unites with its fellow for a short distance, but separates again, passing through the internal carotid foramen into the cranium to supply the brain. Outside the carotid root yet another artery arises

from the first efferent branchial vessel. This is the spiracular or hyoidean artery, which starts in a line with the horizontal vessels that join the loops, runs forwards to the spiracle, where it supplies the pseudobranch, crosses the orbital floor, enters the cranium by a small foramen in the inner wall of the orbit, and joins the internal carotid artery. The dorsal aorta ends in front by breaking into two small prolongations that curve outwards and join the carotid roots, forming the definitive carotid arteries. Just before the dorsal aorta is joined by the last pair of epibranchial vessels it gives off a pair of subclavian arteries, which pass backwards and outwards to the fore-fins. Behind the pharynx it runs backwards along the whole length of the body below the backbone, lying, in the tail, in the hæmal canal as the caudal artery. Besides paired vessels to the body-wall, it gives off to the viscera several median vessels, known successively as the cœliac (of which the hepatic is a branch), anterior mesenteric (of which the genital is a branch), lienogastric, and posterior mesenteric, and to the kidneys several paired renal arteries.

VEINS

The sinus venosus (Fig. 21.15) receives the whole of the blood returning to the heart by a number of very large veins which are called sinuses, though, unlike the sinuses of the arthropods, they do not take the place of capillaries as well as veins in the circulation, but are merely enlarged parts of the veins. The blood from the liver returns direct to the sinus venosus by two hepatic sinuses which enter its hinder side. The rest of the blood is returned by two large ductus Cuvieri [1] which join the sinus venosus, one on each side in the pericardium. Into these the blood from the region of the body in front of the fore-fins is conveyed by a pair of large dorsal anterior cardinal sinuses and two smaller external or inferior jugular sinuses, below the throat. Each anterior cardinal sinus communicates in front with an orbital sinus around the eye, and this in turn with a nasal sinus around the olfactory organ. A hyoidean sinus in the hyoid arch joins the anterior cardinal and inferior jugular. At the outer end of each ductus Cuvieri a subscapular sinus enters from the fore-fin. On its hinder side a very large posterior cardinal sinus brings back blood from the trunk. The two posterior cardinal

[1] '*Ductūs*' is a fourth, not second, declension Latin noun, and its plural is '*ductūs*,' *not* '*ducti*'.

sinuses converge backwards, growing narrower, and lie side by side between the kidneys, from which blood passes into them by numerous renal veins. On each flank two lateral sinuses return blood from the body-wall, and into one of these open vessels from the fins. Blood from the tail is returned by the caudal vein ; this divides opposite the hinder ends of the kidneys into two renal portal veins, which run forwards along the outer sides of the kidneys and supply them with blood. A portal vein is one which takes blood from one set of capillaries to another, and is

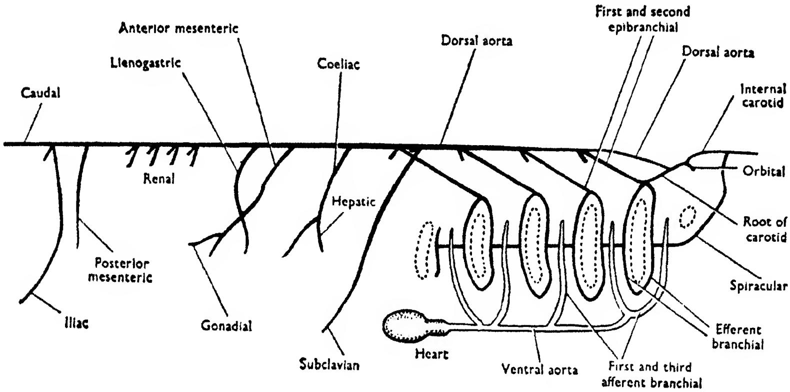


FIG. 21.14.—Dogfish. A diagram of the arterial system, from the right side. The left afferent branchials are omitted and the roots only of other arteries of the left side are shown.

named from the organ in which the second set is situated. Blood from the alimentary canal and spleen is conveyed to the liver by a hepatic portal vein, and thence, after passing through capillaries, is discharged into the hepatic sinuses. It will be noticed that the circulation of the dogfish makes a single circuit only, the blood oxygenated in the respiratory organs being carried directly to the rest of the body without first returning to the heart as in animals with lungs : the pressure of this blood is therefore low. The blood cells of the dogfish resemble those of the frog.

EXCRETION

The kidneys lie outside the peritoneum above the abdominal cavity, and extend for its whole length (Figs. 21.16, 21.17) ; they are wider posteriorly than in front, and in the female the narrow anterior part is vestigial. The kidney consists of a mass of minute tubules, many of which have a small opening, the peritoneal

funnel, into the cœlom ; the vertebrate kidney is made in fact of a series of cœlomoducts, comparable to those of annelids and

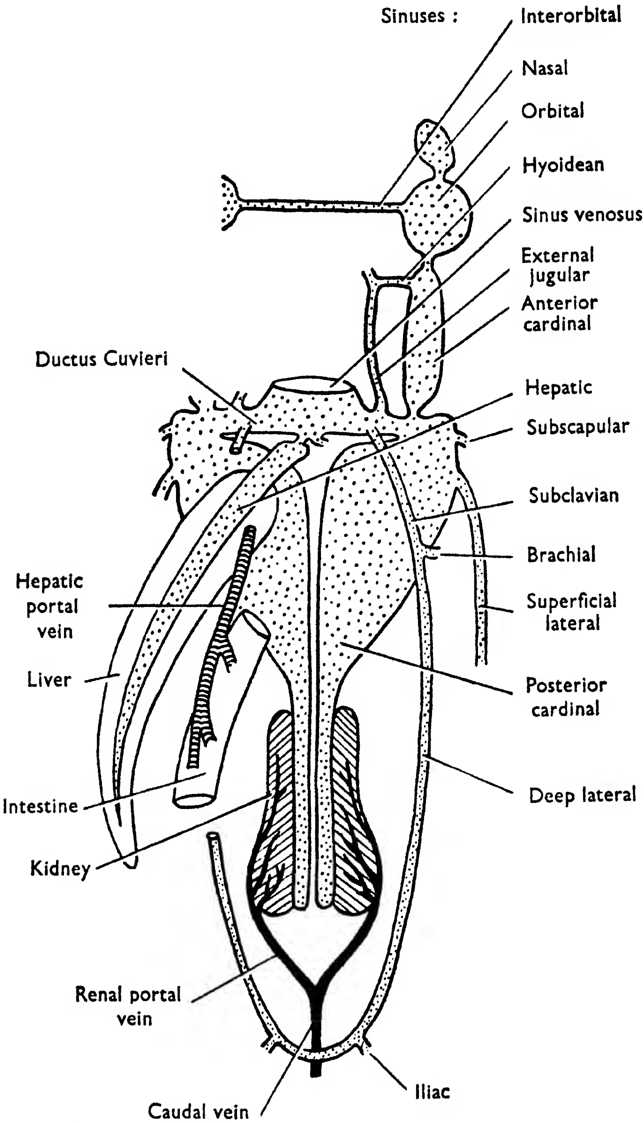


FIG. 21.15.—Dogfish. A diagram of the venous system from the ventral surface. Most of the heart has been removed and some of the vessels are shown on one side only.

arthropods but not homologous with nephridia. At their outer ends the tubules of the anterior part open into a Wolffian duct which runs on the ventral surface of the kidney, and the tubules

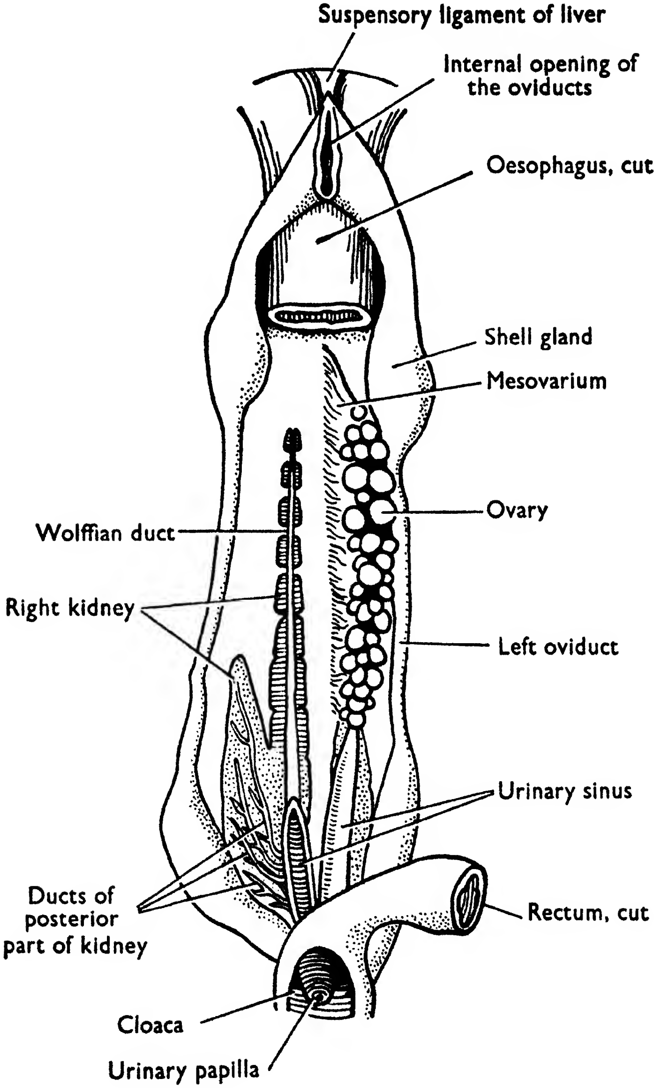


FIG. 21.16.—*Scyllium canicula*. The female urogenital organs dissected from the ventral surface. The ovary has been displaced to the left and the left kidney is not shown. × 1.

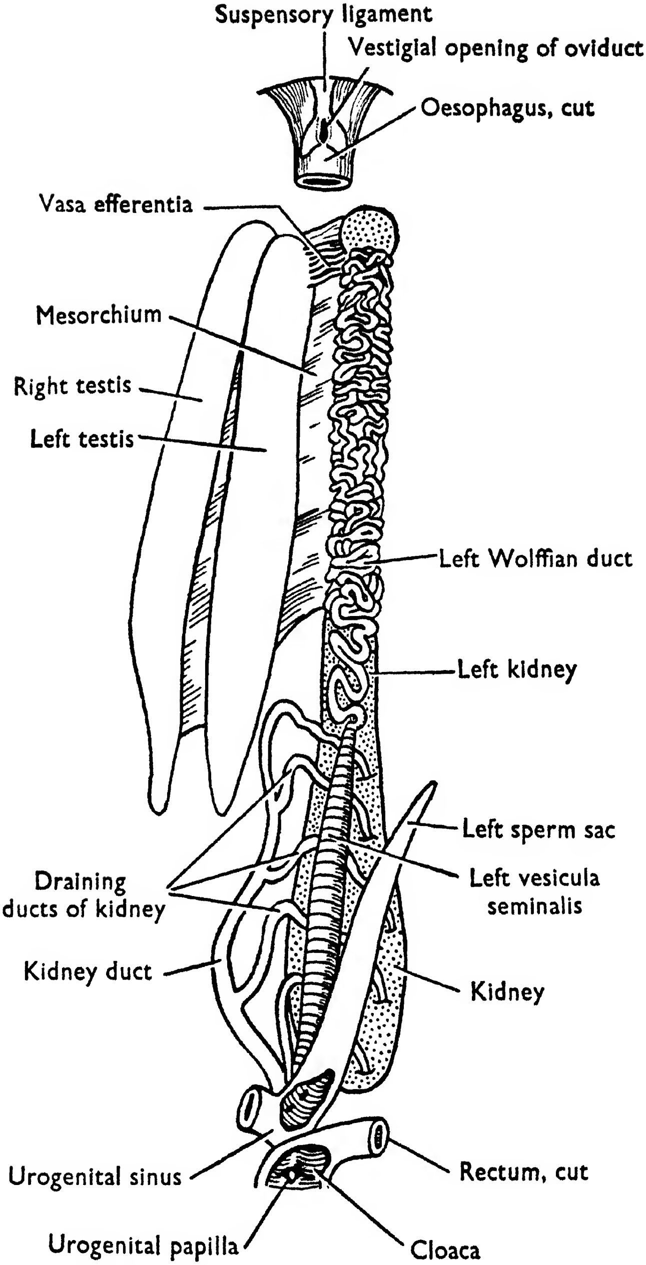


FIG. 21.17.—*Scyllium canicula*. The male urogenital organs dissected from the ventral surface. The testes are displaced to the right and the right kidney is not shown. × 1.

of the hinder part into five or six urinary ducts. In the female the Wolffian duct is straight, and widens at its hinder end to form a urinary sinus, which joins its fellow to open into the cloaca upon a median urinary papilla; the urinary ducts open separately into the urinary sinus. The Wolffian duct of the male is coiled, and, as is usual in vertebrates, receives also the products of the testis; its posterior part is swollen to make a seminal vesicle, which opens into a urogenital sinus. The urinary ducts unite to form a single duct (often miscalled the ureter) which also opens into the urogenital sinus; this has two blind forward-running diverticula, the sperm sacs, lying on the ventral surfaces of the seminal vesicles, and opens into the cloaca on a urogenital papilla. The sperm sacs represent the oviducts of the female.

The principal end-products of nitrogenous metabolism are urea and trimethylamine oxide. Much of these, however, are retained in the blood so that its osmotic pressure is much the same as that of sea-water and the fish have no regulatory problems (p. 192).

REPRODUCTION

There is a single ovary, which is probably that of the right side. It hangs into the body cavity and varies in size and appearance with age. The ova are in different stages of ripeness, the ripest being very large and yolky. They are shed into the body cavity and passed forwards by contractions of the abdominal walls to the front of the peritoneal space where they enter the internal opening of the oviducts. The latter are large straight tubes, one on each side of the body, attached to the dorsal wall of the cœlom. They start from a common opening in the suspensory ligament, not far behind which each has a round swelling known as the shell gland, by which the shells of the eggs are secreted. At the hinder end of the trunk they enter the cloaca by a common opening just behind the anus. The testes are a pair of long organs slung by membranes from the dorsal wall of the cœlom. Each communicates at its front end with the kidney of its side by several small vasa efferentia, the sperms passing through these into kidney tubules and thence to the vas deferens or Wolffian duct, by which it is conveyed to the urogenital sinus. A rudiment of the internal opening of the oviducts is found in the suspensory ligament of the male. Fertilisation is

internal, and there is a form of copulation in which the bodies of the partners are spirally twisted together with the heads back-to-back ; the claspers are stiffened or erected under the influence of adrenaline (p. 16) and inserted into the cloaca of the female, where the dilatation of their terminal parts holds the fishes together. It is possible that the semen is washed out of the grooves of the claspers by sea water injected into them by the 'siphon', a muscular sac which lies under the skin of the

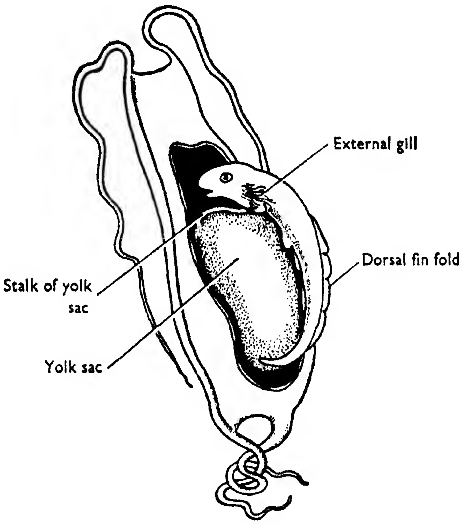


FIG. 21.18.—*Scyllium canicula*. A mermaid's purse cut open to show the embryo. × 0.5.

ventral surface in the pelvic region and communicates by two channels with the grooves. Sperms are stored in the folds of the shell gland. In the Bristol Channel the spawning season starts in November and lasts at least until the following July ; sexual activities take place in shallow water.

The eggs of *Scyllium* are laid in flat, oblong, brown shells (or mermaids' purses), the angles of which are prolonged into tapering tendrils, which twine round seaweeds and thus anchor the egg (Fig. 21.18). Protected by the shell, the young dogfish develops slowly at the expense of the yolk, which comes to be contained in a sac attached to its belly. At one stage long, vascular threads project from the gill clefts of the little fish. These are the so-called external gills, but they are covered with endoderm

and thus differ from the true external gills of the tadpole. *Acanthias* is viviparous—that is, the eggs hatch internally. The embryo is nourished through vascular and secretory ridges on the walls of the oviduct.

NERVOUS SYSTEM

The spinal cord of the dogfish has the general features of that of a vertebrate as seen in a mammal (p. 538) and will not be described here. The brain also has the same parts, but differs

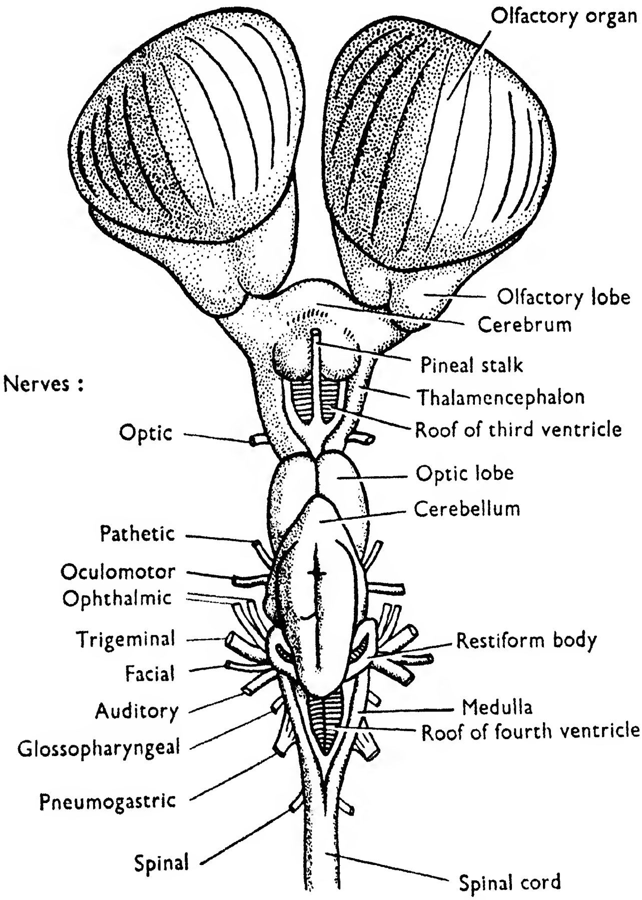


FIG. 21.19.—*Scyllium canicula*. The brain in dorsal view. × 1.5.

from that of a mammal in not being bent; the shape and relationship of the parts are shown in Figs. 21.19 and 21.20. The anterior cerebrum is not divided into the two hemispheres of the mammal, but has two internal cavities or lateral ventricles. These extend into the olfactory lobes, which are large and extend forwards from the anterior corners of the cerebrum to press against the

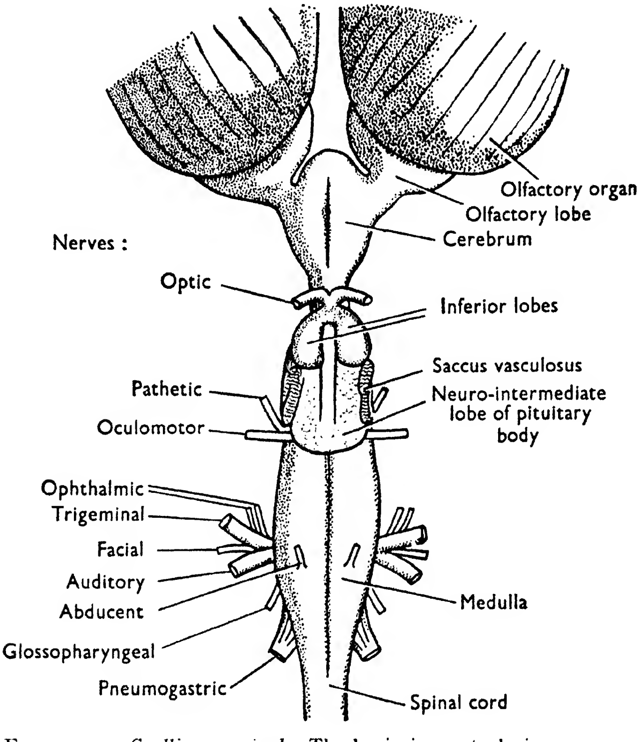


FIG. 21.20.—*Scyllium canicula.* The brain in ventral view. × 1.5.

olfactory organs, which are covered by the olfactory capsules. Behind the cerebrum comes a long thalamencephalon, with a thin roof from the hinder part of which rises the pineal stalk ; this runs forward to end in a pineal body below the anterior fontanelle. From the floor of the thalamencephalon the infundibulum extends downwards ; at its sides are a pair of inferior lobes, and behind these it forms the saccus vasculosus and the nervous part of the pituitary body (p. 470). The cavity of the thalamencephalon is the third ventricle. Behind the thalamencephalon is

the midbrain, with two large dorsal optic lobes, and behind this again a large cerebellum. This is succeeded by the medulla oblongata, with thin roof and a pair of restiform bodies projecting forward from it alongside the cerebellum. The cavity of the

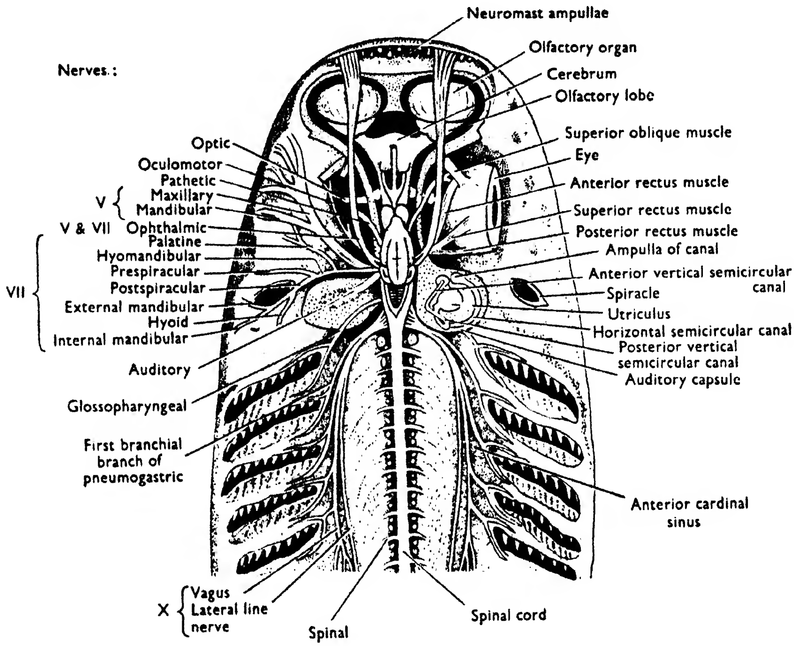


FIG. 21.21.—*Scyllium canicula*. The head dissected from the dorsal surface to show the brain and nervous system. The skull is shown with large dots; the left eye and most of the left auditory capsule have been removed. × 1.

cerebellum and medulla is the fourth ventricle ; this is connected to the third ventricle by a narrow passage in the midbrain, the aquaeductus Sylvii or iter a tertio ad quartum ventriculum, or iter for short.

The central nervous system gives off paired nerves, and in the trunk and tail these are obviously segmentally arranged. forming the series of spinal nerves characteristic of vertebrates. Each nerve has a dorsal root, consisting of sensory fibres, which goes out of the neural canal by a notch in the hind edge of the intercalary piece, and a ventral, of motor fibres, which goes out by a notch in the hind edge of the neural arch. The dorsal root

has a ganglion just outside the vertebra, and beyond this the two roots join. The common nerve thus formed divides at once into a short dorsal branch to the muscles and skin of the back, and a long ventral branch to the rest of the segment. There is

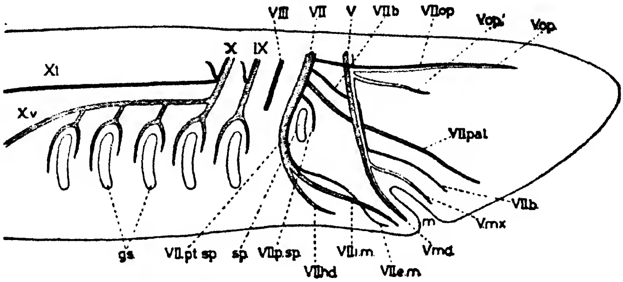


FIG. 21.22.—A diagram of certain cranial nerves in the dogfish. The nerves omitted (III, IV, VI) consist of motor fibres to the eye muscles. Those shown supply the visceral arches and certain other parts. They contain (*a*, shaded) visceral motor (autonomic) and visceral sensory fibres; (*b*, black) fibres from the neuromast system (p. 342) and ear; and (*c*, white), chiefly in V, some other somatic sensory fibres from the skin.

V., *VII.-X.*, Roots of the nerves; *V.md.*, *V.mx.*, *V.op.*, mandibular, maxillary, and superficial ophthalmic branches of the fifth nerve; *V.op'.*, deep ophthalmic nerve, inconspicuous in the rough hound, but large in many other fishes (p. 577); *VII.b.*, *VII.e.m.*, *VII.hd.*, *VII.i.m.*, *VII.op.*, *VII.pal.*, buccal, external mandibular, hyoidean, internal mandibular, ophthalmic and palatine branches of the seventh nerve; *VII.p.sp.*, *VII.pt.sp.*, pre- and post-spiracular divisions of hyomandibular branch of seventh nerve; *X.l.*, *X.v.*, lateral line and main visceral branches of the tenth nerve; *g.s.*, gill slits; *m.*, mouth; *sp.*, spiracle.

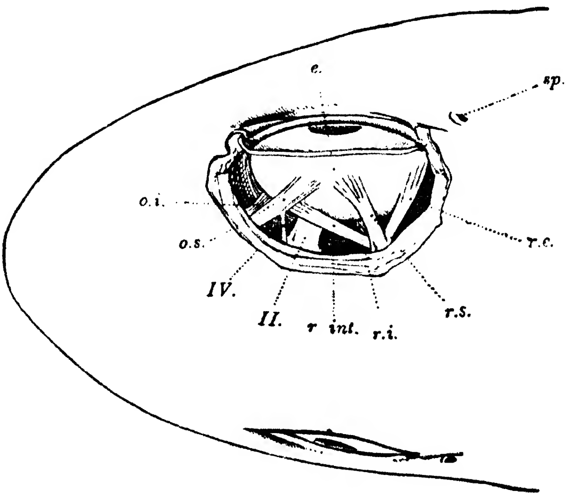


FIG. 21.23.—The head of a dogfish, seen from above with the right orbit opened.

e. Eyeball; *o.i.*, *o.s.*, inferior and superior oblique muscles; *r.e.*, *r.i.*, *r.int.*, *r.s.*, external, inferior, internal and superior recti muscles; *sp.*, spiracle; *II.*, optic nerve; *IV.*, fourth nerve.

also a short ramus communicans (plural rami communicantes) to the sympathetic system. This is a series of connected ganglia,

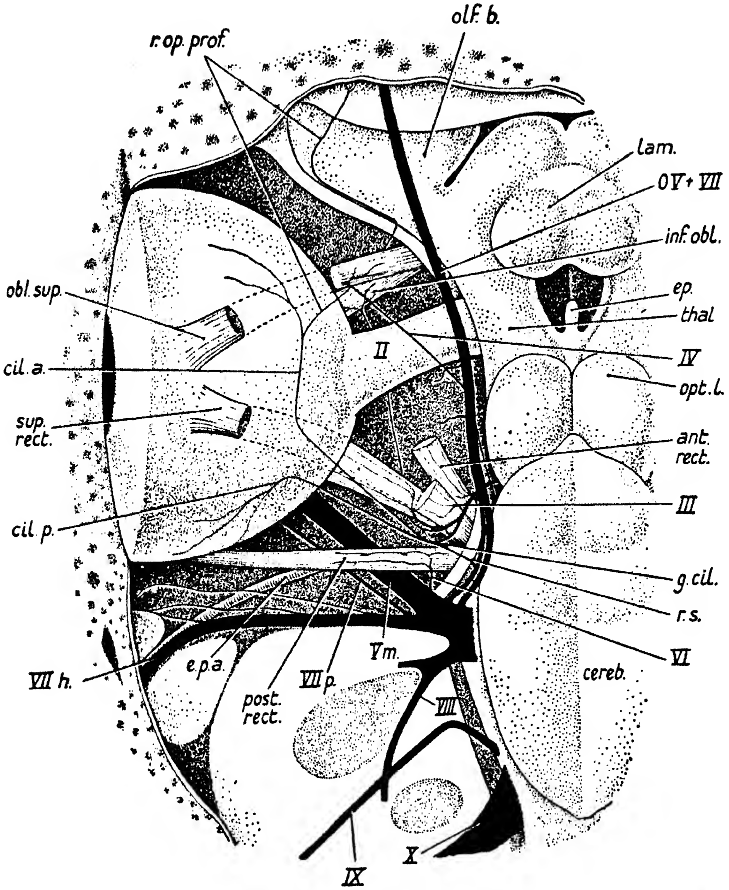


FIG. 21.24.—Left orbit of the dogfish (*Scyliorhinus*) dissected from above. Parts of some of the eyeball muscles have been removed.—From Young, *The Life of Vertebrates*, 1950. Clarendon Press, Oxford.

ant. rect., Rectus anterior; *cereb.*, cerebellum; *cil.a.*, *cil.p.*, anterior and posterior ciliary nerves; *e.p.a.*, efferent pseudobranchial artery; *ep.*, epiphysis; *g.cil.*, ciliary ganglion; *inf.obl.*, obliquus inferior; *lam.*, lamina terminalis; *OV+VII.*, superficial ophthalmic; *obl. sup.*, obliquus superior; *olf.b.*, olfactory bulb; *opt.l.*, optic lobe; *post. rect.*, rectus posterior; *r.op. prof*, deep ophthalmic branch of trigeminal; *r.s.*, sensory root of ciliary ganglion; *sup. rect.*, rectus superior, mostly cut away to show the rectus inferior lying below it; *thal.*, thalamus; *II–X*, cranial nerves (*vm.*, maxillary and mandibular; *VIIh.*, hyomandibular; *VIIp.*, palatine).

approximately segmentally arranged, situated above the posterior cardinal sinus, and giving motor fibres to the viscera. Each fin is supplied by a group of ventral branches forming a plexus.

The detailed organisation of the nervous system is discussed in Chapter 27.

The cranial nerves (Figs. 21.21, 21.22), which arise inside the skull, also have dorsal and ventral roots, and are also segmentally arranged, but because their roots do not join, and because the development of the sense capsules has obscured the segmentation of the head, their proper plan was for long unrecognised and they are traditionally described as a single series of paired nerves

TABLE IV.

The Cranial Nerves of the Dogfish

Conventional Number	Name	Origin and distribution	Chief fibres
O.	Terminal	From forebrain to snout.	Somatic sensory
I.	Olfactory	Multiple ; from olfactory lobes to olfactory organs.	
II.	Optic	From optic lobes by the thalamencephalon and chiasma to eye.	
III.	Oculomotor	From ventral surface of midbrain to four eyeball muscles : rectus anterior, rectus superior, rectus inferior, obliquus inferior.	Somatic motor
IV.	Pathetic or trochlear	From dorsal surface between optic lobes and cerebellum to obliquus superior muscle.	Somatic motor
V.	Trigeminal	From medulla, as all the rest. Inside the skull it has a Gasserian ganglion. Four main branches.	
		1. Superficial ophthalmic ; through orbit, over olfactory lobe to skin of snout.	Somatic sensory
		2. Maxillary ; through orbit to upper jaw.	Visceral motor and somatic sensory
		3. Mandibular ; to lower jaw, lips.	Visceral motor and sensory
		4. Profundus or deep ophthalmic ; small, and usually described as absent, which it is in some specimens of *Scyliorhinus*. To eyeball, and then forward below V.1 to snout.	Somatic sensory
VI.	Abducent	To rectus posterior muscle of eyeball ; very small.	Somatic motor

TABLE IV.—*Continued*

Conventional Number	Name	Origin and distribution	Chief fibres
VII.	Facial	Inside the skull it has a geniculate ganglion. Four main branches.	
		1. Superficial ophthalmic; close to that of V.	Lateral line
		2. Buccal; across orbit with maxillary branch of V, and then to infraorbital region.	Lateral line
		3. Palatine; through orbit behind maxillary branch of V and mandibular branch of V to roof of mouth. Small.	Visceral sensory
		4. Hyomandibular; divides into:	
		4.1 Prespiracular; small.	Visceral sensory
		4.2 Postspiracular, which divides into:	
		4.21 Internal mandibular; mucous surface of lower jaw and mouth.	Visceral sensory
		4.22 External mandibular; to hyoid region.	Visceral motor, visceral sensory, and lateral line, the first two parts being sometimes distinguished as the hyoidean.
VIII.	Auditory	To ear.	Lateral line
IX.	Glosso-pharyngeal	Its ganglion is the petrosal; to 1st gill cleft; pre- and post-trematic branches before and behind cleft respectively, and dorsal pharyngeal branch.	Visceral sensory fibres in all, and visceral motor in the post-trematic.
X.	Pneumo-gastric or vagus	Its ganglion is the vagus or jugular; many roots, to remaining gill clefts.	
		1. Four branchial branches with distribution and composition as in IX.	
		2. Lateral line nerve.	Lateral line
		3. The main part continues as the intestinal or visceral branch, to gut and heart.	Visceral sensory and motor
XI.	Spinal accessory	Absent from the dogfish.	
XII.	Hypoglossal	Absent from the dogfish.	

numbered from nought to ten (or, in some animals, twelve). Their segmental arrangement, which has been known since the work of F. M. Balfour, A. M. Marshall, and J. W. van Wighe in the eighteen-seventies and early eighties, is described in Chapter 27; the old numbering, which is still convenient in dissection, is shown in Table IV. The chiasma in the optic nerve is a crossing-over of the fibres from the eye of one side to the optic lobe of the other. The distinction of fibres as visceral or somatic is explained in Chapter 27.

Each of the olfactory organs of the dogfish is a sac enclosed in the olfactory capsule; it opens externally by the nostril, but has no internal opening. Its walls are thrown into vertical folds covered with an epithelium which contains sense cells which respond to odours. On the wall of the pharynx are taste buds which are said to be capable, like those of man, of distinguishing between saltness, sweetness, sourness, and bitterness. The eyes have the same general structure as those of mammals (p. 464) and each is held in position by six eyeball muscles (Figs. 21.23 and 21.24). In the front of the orbit is a pair, the obliquus superior and obliquus inferior, and behind these are four, arranged as a cross: the rectus internus, or anterior; the rectus externus, or posterior; the rectus superior, and the rectus inferior. The lens is spherical, and as it has a muscle which can move it forwards it may be assumed that accommodation is carried out in this way. The retina contains only rods. The internal ear has semicircular canals, sacculus and utriculus, but lacks the other parts present in higher vertebrates. It is undoubtedly an organ of balance, but there is no evidence that the dogfish can hear. Related to the semicircular canals is the system of lateral line or neuromast organs, supplied by branches of the seventh, ninth and tenth nerves. The sense cells of the system are situated in pits and tubes in the skin filled with mucus, and opening to the exterior at intervals. The most conspicuous of them is the lateral line itself, which is visible as a streak of pigment all the way down the side of the body. The sense cells respond to temperature changes and chiefly to any movements in the water which affect the fluid in the tubes. The lateral line system is of great importance in fishes, but is absent from terrestrial vertebrates. The ear appears to be derived from the lateral line system, and the two together are called the acustico-lateralis system.

DUCTLESS GLANDS

Finally, we may note the condition of the ductless glands (p. 16) in the dogfish. With the thyroid and the pituitary body we have already dealt (pp. 325, 336). The thymus is present as lobed masses of glandular tissue above the gill clefts, from whose epithelium it arises during development, as in all vertebrates. The adrenal bodies are represented by two separate elements. Between the kidneys an elongate structure, the interrenal body, derived from the cœlomic epithelium, represents the cortex of the adrenals of the frog and higher vertebrates ; on the course of the sympathetic chains a number of bodies of the same origin as the cells of the sympathetic ganglia represent the medulla of the adrenals. These bodies are the suprarenals.

22

THE FROG

THE common frog of Britain, *Rana temporaria,* is abundant in summer in damp places, but in winter is less easily found, owing to the fact that it is then in a torpid state, hidden in holes or buried in mud. It lives principally on land, either crawling about by means of

FIG. 22.1.—The common frog.

both pairs of limbs or jumping with the strong hinder pair and using the small fore pair to break its fall when it alights, but it can swim strongly with its hind limbs. Its food consists largely of insects and molluscs with worms and other small animals, the smaller prey being caught by a sticky tongue, the larger seized with the mouth.

EXTERNAL FEATURES

The mottled green and yellow skin is soft and slimy and without the covering of hairs, or scales, or feathers which we find in other vertebrates, and the body consists only of head, trunk, and two pairs of limbs. There is no neck or tail. The eyes are large, and have stout, almost immovable upper lids and thin, translucent, movable lower lids which are different in structure from

those of man. The nostrils or external nares are a pair of small openings on the top of the head in front of the eyes. Each of them leads into a chamber which communicates with the mouth.

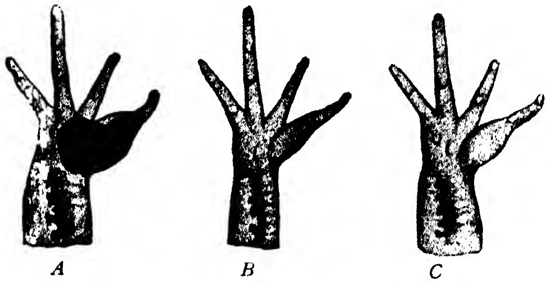


FIG. 22.2.—The right hand of a frog : *A*, male at breeding season ; *B*, female ; *C*, male out of breeding season.

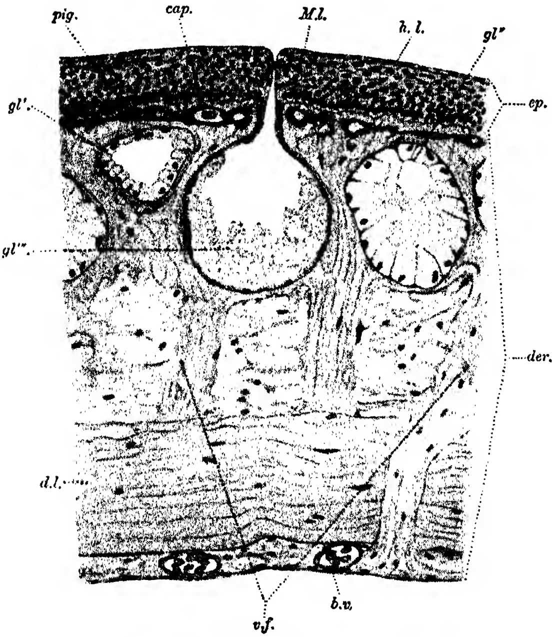


FIG. 22.3.—A section of the skin of a frog, taken vertically to the surface, highly magnified.

b.v., Small blood vessels ; ***cap.***, capillaries ; ***d.l.***, dense layer of connective tissue, consisting of fibres which lie parallel to the surface ; ***der.***, dermis or corium ; ***ep.***, epidermis ; ***gl'.***, ***gl''.***, ***gl'''.***, glands of three kinds ; ***gl'.*** and ***gl''.*** secrete a slimy mucus and pass it to the surface of the skin by ducts which are not shown in the section ; ***gl'''.*** secretes a more watery secretion which probably contains a substance of unpleasant taste ; all three kinds are simple glands of the saccular type ; ***h.l.*** horny layer of the epidermis ; ***M.l.***, lowest row of the Malpighian layer of the epidermis ; ***pig.*** pigment cells ; ***v.f.***, strands of vertical fibres in the connective tissue.

There is no flap to the ear, but the drum shows upon the surface at the side of the head behind and somewhat below the eye. If the drum be pierced, a bristle passed through it will be found to reach the mouth. On the lower side of the trunk there may be distinguished two regions—the large, soft-walled belly or abdomen behind, and the smaller stout-walled breast region in front.

The hand has only four digits, that which corresponds to the thumb of man being absent. The first finger of the male frog bears at the breeding season a rough-skinned swelling, not unlike the ball of the human thumb (Fig. 22.2). The ankle is much longer than the wrist, and all five toes are present and united by webs of skin, so that a wide surface is provided for use in swimming.

Between the legs at the hinder or posterior end of the trunk is the vent or cloacal opening, through which are passed the fæces, urine, and eggs or sperms.

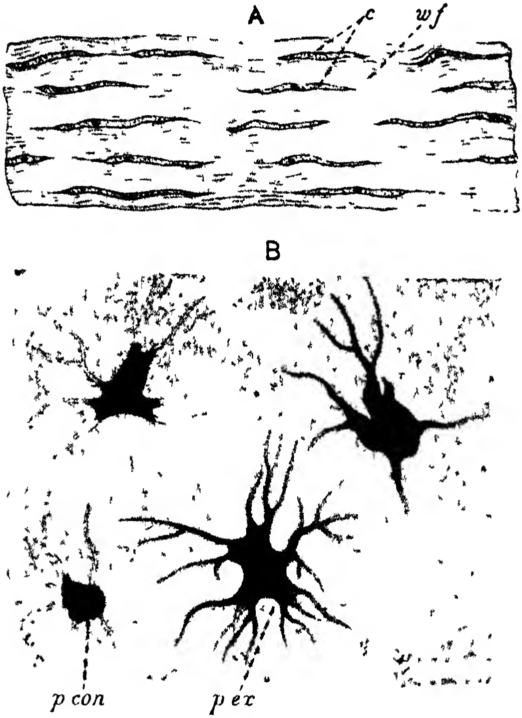


Fig. 22.4.—Connective tissues of the frog.

A, Tendon; *B*, pigment cells in the skin, seen through the epidermis. *c*, Cells; *p con*, pigment cell with the pigment contracted; *p ex*, pigment cell with the pigment extending into the processes; *w f*, white fibres.

SKIN

The skin of the frog is a thin, tough, protective covering. The dermis or inner layer contains pigment cells or melanophores (Figs. 22.3, 22.4 B), and embedded epidermal glands of several kinds which between them give a slimy liquid that possesses slightly the acrid property found in the secretion of the skin of toads and newts. By its evaporation it cools the frog, which in air is always at a slightly lower temperature than its surroundings. The pigment in the cells is dispersed or concentrated in varying conditions of light, temperature, etc., and thus the colour of the frog changes (p. 366). Cold, dark, or wet surroundings cause dispersion of the pigment and darkening of the skin. Warmth, light, or dryness cause concentration. From time to time, under the stimulus of secretions of the thyroid and pituitary glands, the horny outer layer of the epidermis is shed and eaten by the frog.

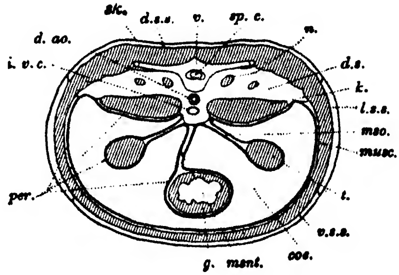


FIG. 22.5.—A diagram of a transverse section through the abdomen of a male frog.

coe., Cœlom ; *d.ao.*, dorsal aorta ; *d.s.*, dorsal lymph sac ; *d.s.s.*, dorsal subcutaneous lymph sac ; *g.*, gut ; *i.v.c.*, inferior vena cava ; *k.*, kidney ; *l.s.s.*, lateral subcutaneous lymph sac ; *msnt.*, mesentery ; *mso.*, mesorchium ; *musc.*, muscular body-wall ; *n.*, spinal nerves ; *per.*, peritoneum ; *sk.*, skin ; *sp.c.*, spinal cord ; *t.*, testis : *v.*, vertebra *v.s.s.*, ventral subcutaneous lymph sac.

GENERAL ARRANGEMENT OF INTERNAL ORGANS

Immediately below the skin is a series of large spaces, the subcutaneous lymph sacs (Fig. (22.5). Between the lymph sacs the skin is bound down to the underlying flesh by tough, white connective tissue, but in consequence of the presence of the sacs it is much looser than that of most animals. Below the sacs there is a body-wall of muscles enclosing the cœlom. Between the dorsal wall of this and the muscles of the back is a pair of large dorsal lymph sacs in which lie the kidneys.

SKELETON: GENERAL ARRANGEMENT

The skeleton of the frog is composed chiefly of bone, but contains also a good deal of gristle or cartilage. Although it is built on the general vertebrate plan it is very atypical ; most of its peculiarities may be connected with the unusual mode of progression by leaping.

BACKBONE

In the backbone there are nine vertebræ, and a long bone known as the urostyle which represents several vertebræ fused together. Each vertebra has the same general parts as those of

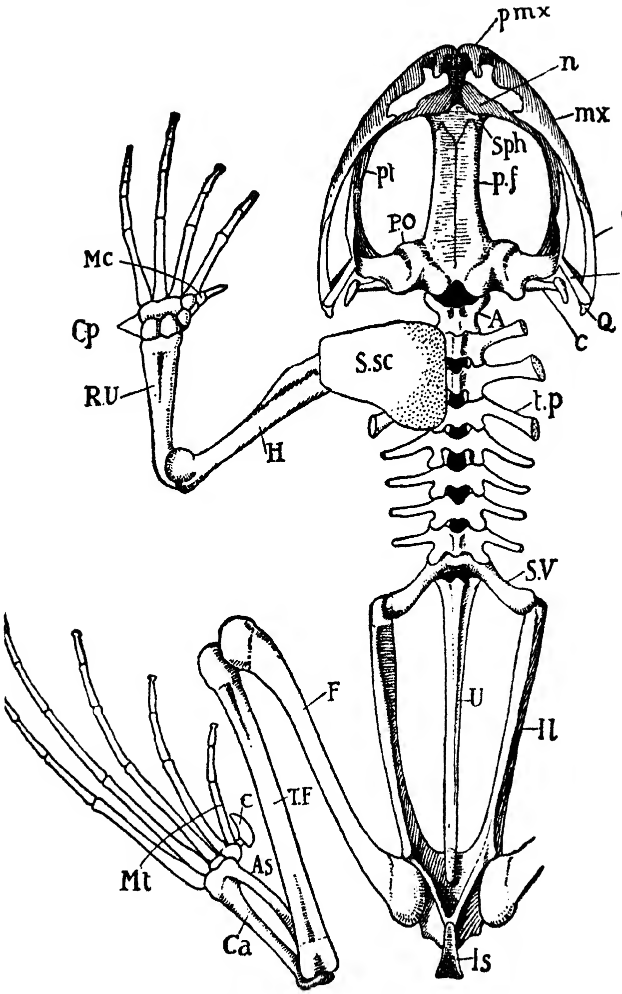


FIG. 22.6.—Skeleton of frog. The half of the pectoral girdle, and fore- and hind-limb of the right side, are not shown.

A., atlas ; *As.*, astragalus ; *C.*, calcar ; *C.*, columella auris ; *Ca.*, calcaneum ; *Cp.*, carpals ; *F.*, femur ; *H.*, humerus ; *Il.*, ilium ; *Is.*, ischium ; *Mc.*, metacarpals ; *Mt.*, metatarsals ; *mx.*, maxilla ; *n.*, nasal ; *p.f.*, fronto-parietal ; *pmx.*, premaxilla ; *P.O.*, pro-otic ; *pt.*, pterygoid ; *Q.*, quadrate ; *q.j.*, quadrato-jugal ; *R.U.*, radio-ulna ; *sph.*, sphenethmoid ; *sq.*, squamosal ; *S.sc.*, suprascapula ; *S.V.*, sacral vertebra ; *T.F.*, tibio-fibula ; *t.p.*, transverse process ; *U.*, urostyle.

the rabbit (p. 419) but there are no ribs, these being represented by small knobs of cartilage on the transverse processes. The centra have traces of a canal for the notochord (p. 301). The typical structure is shown by vertebræ two to seven (Fig. 22.7), in which the centra are procœlous, that is, they are hollow in front and bulged at the back, so that they articulate with one another and the whole series forms a flexible jointed axis. There

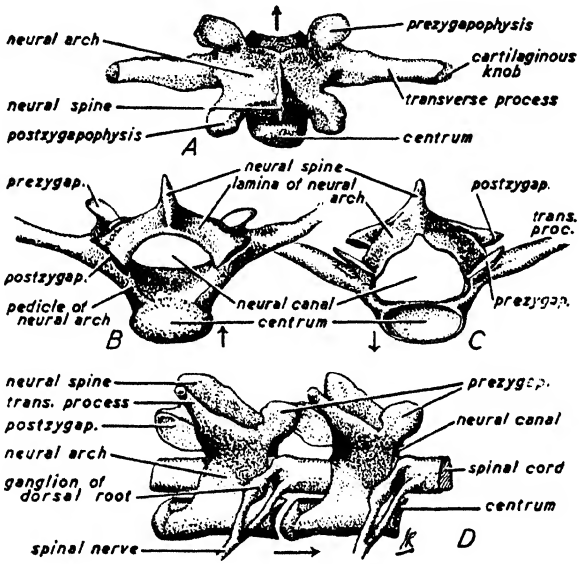


FIG. 22.7.—The structure of a frog's vertebra.—From Thomson.

A, Fifth vertebra from above; *B*, from the posterior; *C*, from the anterior; *D*, side view of fifth and sixth vertebræ, not quite articulated, showing position of spinal cord and spinal nerves. An arrow beside each figure points towards the head.

are certain peculiarities, which enable most of the individual vertebræ to be easily recognised.

The first has its centrum greatly reduced and there are no transverse processes, so that it is little more than a ring of bone; it has two hollows in front which fit the occipital condyles of the skull, and a single bulge behind. It is known as the atlas because it carries the skull just as the giant Atlas of Greek legend carried the world on his shoulders.

The second has its transverse processes directed forwards.

The third has large transverse processes directly outwards at right angles to the whole backbone.

The fourth has large transverse processes directed backwards at an angle of about 45°.

In the fifth, sixth, and seventh, the transverse processes are directed slightly backwards.

The transverse processes of the eighth resemble those of the fifth to seventh but the centrum is amphicœlous, that is, it is hollow both fore and aft.

The ninth has large transverse processes directed backwards to articulate with the ilia (p. 356) ; any vertebra which thus comes in contact with the pelvic girdle is called sacral. The centrum has one knob in front, for the eighth vertebra, and two behind with which it articulates with the urostyle, which is a long, tapering bone with a ridge above, and bearing in its front part a canal for the hind part of the spinal cord.

THE SKULL

The skull of the tadpole consists entirely of cartilage, but in the adult frog, as in the dog (p. 423), bones are formed in the cartilage while other bones, called membrane bones, are applied on the outside. Much cartilage, however, remains. The bones of the skull are best learnt from behind forwards, with the sense capsules considered after the brain-box.

The cranium or brain-box is somewhat brick-shaped, and is made mostly of cartilage (Fig. 22.8). At its hind end is a large opening, the foramen magnum, through which the spinal cord is continuous with the brain. On each side of this the cartilage is replaced by an exoccipital bone, which has a backwardly directed knob, the occipital condyle, but the upper and lower borders of the foramen are not ossified. The only other bone in the cranium is a large sphenethmoid at the anterior end ; it is shaped like a dice-box, with across the waist a transverse partition which makes the front wall of the cranial cavity ; the anterior hollow is divided by a vertical partition. The sphenethmoid corresponds to the mesethmoid, orbitosphenoids and presphenoid of the dog, together with part of the nasal capsule. The roof of the cartilaginous cranium is incomplete, having three gaps or fontanelles, one large anterior and two small posterior, but these are covered by a pair of long membrane bones, the frontoparietals. Below the floor, which is complete, is a dagger-shaped membrane bone, the parasphenoid, with its handle directed backwards.

The wall of the cranium has a number of openings or foramina, for the passage of the nerves and arteries. The first cranial nerve of each side passes through a foramen in the transverse partition of the sphenethmoid on its way from the organ of smell in the nasal capsule. The second nerve, which serves the eye, enters the skull through a conspicuous opening on each side in the middle of the sphenoidal region. The third and fourth nerves have each a minute foramen in the side of the same region. The fifth and seventh nerves pass through a large common opening on the under side of the skull, situated in a notch in the pro-otic bone mentioned below. The foramen for the sixth nerve is a small opening between those for the second and for the fifth and seventh. The eighth nerve enters from the inner part of the ear by an opening in the wall between the cranium and the auditory capsule. A foramen for the ninth and tenth nerves is situated in the exoccipital bone, at the side of the occipital condyle.

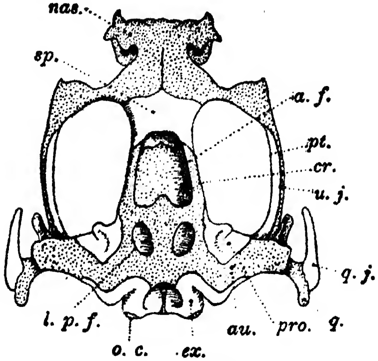


FIG. 22.8.—The cartilaginous skull of a frog, seen from above after the removal of most of the bones.

a.f., Anterior fontanelle ; *au.*, auditory capsule ; *cr.*, cranium ; *ex.*, exoccipital ; *l.p.f.*, left posterior fontanelle ; *nas.*, nasal capsule ; *o.c.*, occipital condyle ; *pro.*, pro-otic ; *pt.* pterygoid ; *q.*, quadrate ; *q.j.*, quadratojugal ; *sp.*, sphenethmoid, *u.j.*, upper jaw bar.

The auditory capsules are blocks of cartilage continuous with that of the cranium, and applied to its posterior corners. Each contains a complicated space, the cartilaginous labyrinth, which lodges a structure known as 'the membranous labyrinth of the ear'. Part of the front of the capsule is ossified to form the pro-otic

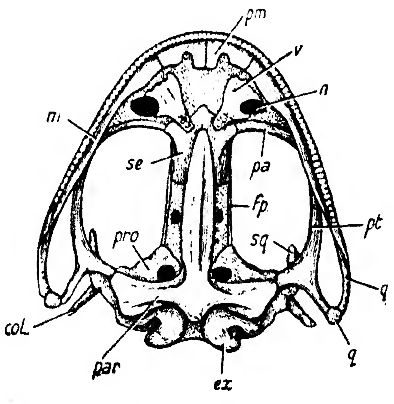


FIG. 22.9.—Skull of frog, ventral.—From Young, *The Life of Vertebrates*, 1950. Clarendon Press, Oxford. After Marshall.

col., Columella auris ; *ex.*, exoccipital ; *f.p.*, fronto-parietal ; *m.*, maxilla ; *n.*, nostril ; *pa.*, palatine ; *par.*, parasphenoid ; *pm.*, premaxilla ; *pro.*, pro-otic ; *pt.*, pterygoid ; *q.*, quadrate ; *qj.*, quadrato-jugal ; *se.*, sphenethmoid ; *sq.*, squamosal ; *v.* vomer.

bone. Above, there abuts on its outer side a T-shaped membrane bone known as the squamosal, which touches it by one limb of the cross-piece of the T, the main limb being directed outwards and downwards. At one spot on the outer side of the capsule a separate piece of cartilage fits into a membrane-covered gap known as the fenestra ovalis, and from it a slender rod of bone and cartilage, homologous with the hyomandibula of fishes, but here called the columella auris, runs to the drum of the ear, so that when the latter is thrown into vibrations by sound waves

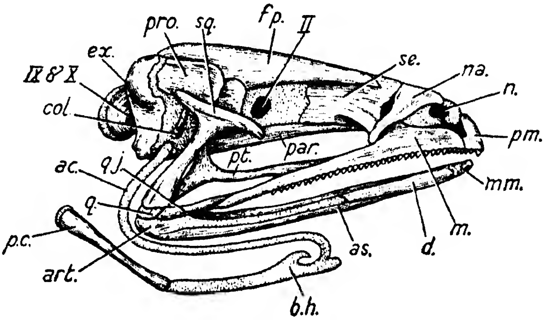


FIG. 22.10.—Skull of frog, side view.—From Young, *The Life of Vertebrates*, 1950. Clarendon Press, Oxford.—After Marshall.

ac., Anterior horn of hyoid ; *art.*, articular ; *as.*, angulosplenial ; *b.h.*, body of hyoid ; *col.*, columella auris ; *d.*, dentary ; *ex.*, exoccipital ; *fp.*, frontoparietal ; *m.*, maxilla ; *mm.*, mentomeckelian ; *n.*, nostril ; *na.*, nasal ; *par.*, parasphenoid ; *p.c.*, posterior horn of hyoid ; *pm.*, premaxilla ; *pro.*, pro-otic ; *pt.*, pterygoid ; *q.*, quadrate ; *qj.*, quadratojugal ; *se.*, sphenethmoid ; *sq.*, squamosal ; *II*, *IX*, *and X*, foramina for cranial nerves.

its movements are transferred by the columella through the membrane to the inner ear which lies beneath it.

The nasal capsules are a pair of irregular, mainly cartilaginous, enclosures continuous with the front end of the cranium. Only their hinder part is ossified, and this forms that part of the sphenethmoid which lies in front of the transverse partition of the latter. The wall between the two capsules is known as the mesethmoid. Through these capsules run the passages from the nostrils to the mouth, and each of them has therefore an opening above and below. Each bears two membrane bones, one on its upper side and one beneath. The upper bone is known as the nasal, and is shaped like the outline of a pear, with the stalk directed outwards. The lower, usually called vomer, is also called prevomer, because of doubt as to its homology with the vomer of mammals. It is of irregular shape and carries a patch of teeth which project through the skin of the roof of the mouth.

The front part of the upper jaw is closely applied to the nasal capsule, but behind it diverges widely, to make a large space, the orbit, between the jaw and the cranium. In the orbit is the eye.

The primary cartilaginous upper jaw remains unossified at its posterior end as a small quadrate, which articulates with the lower jaw and is held firm above by the squamosal. In front the cartilage partially ossifies to form a pterygoid and a palatine, but in the group of animals to which the frog belongs these cartilage bones are lost and replaced by membrane bones to which the same names are given. The pterygoid is Y-shaped, with the fork directed backwards, the inner arm abutting on the auditory capsule and the outer on the quadrate, which it helps to hold against the squamosal. The palatine runs transversely from the anterior end of the pterygoid to the sphenethmoid. The cartilage of the jaw runs forward from the quadrate as a continuous bar on the outside of the pterygoid bone and in front of the palatine. A second series of membrane bones is situated outside the primitive jaw, and borders the opening of the mouth. In contact with the quadrate and squamosal is a small quadratojugal, and from this runs forwards a long maxilla, which bears teeth, and is in contact in front with the nasal capsule and pterygoid. In front of the maxilla is a small premaxilla, also with teeth, which rests on the front of the nasal capsule. The two premaxillæ touch in front.

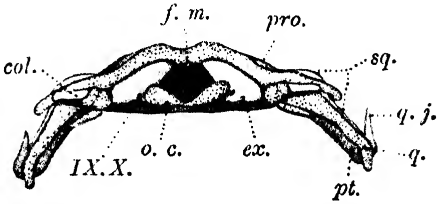


FIG. 22.11.—The skull of frog, seen from behind.

col. Columella ; *ex.*, exoccipital ; *f.m.*, foramen magnum ; *o.c.*, occipital condyle ; *pro.*, pro-otic ; *pt.*, pterygoid ; *q.*, quadrate ; *q.j.* quadratojugal ; *sq.*, squamosal ; *IX.X.*, foramen for ninth and tenth cranial nerves.

The lower jaw or mandible consists of two halves united in front by a ligament. Each half is a curved rod of cartilage, known as Meckel's cartilage, ossified at the anterior end to form the small mentomeckelian bone, and almost completely ensheathed by a couple of membrane bones, the angulosplenial within, and the dentary without. The latter does not, as its name would imply, bear teeth, the frog having no teeth in the lower jaw. At the near end or angle of the jaw, the dentary bears a

small knob or condyle, which fits into a hollow on the end of the quadrate known as the mandibular fossa. Meckel's cartilage appears also to be in contact with the quadrate.

The hyoid (Fig. 21.12) is a flat structure in the floor of the mouth. It consists of a wide body with two short processes on each side and two longer processes, the cornua, at each end. The anterior cornua are very long and slender and curve backwards at the sides of the body and then upwards to be attached to the sides of the auditory capsules. The posterior cornua are shorter and stouter and project backwards at the sides of the windpipe. They are the only ossified parts of the hyoid, the remainder consisting of cartilage. The hyoid, the columella auris, and the cartilages of the larynx probably represent the branchial arches of fishes.

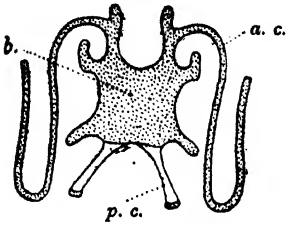


FIG. 22.12.—The hyoid apparatus of a frog.
a. c., Anterior cornua ; *b.*, body ; *p.c.*, posterior cornua.

LIMB GIRDLES

The pectoral or shoulder girdle (Fig. 22.13) is a flattened structure of cartilage and bone embedded in the body-wall of the forepart of the trunk, which it almost encircles. It consists of two similar halves, one on each side of the body united below but separate above, where they are bound by muscles to the backbone. Each half is composed of an upper scapular portion or shoulder blade and a lower coracoid portion. The uppermost part is a broad, flat plate lying on the back known as the suprascapula. A great part of this consists of cartilage stiffened by calcareous matter, but it has a narrow rim of plain cartilage and a patch of true bone lies upon it where it joins the scapula, a narrower but stouter bone placed at the side of the body. A forward projection from this bone is known as the acromion process. To the lower end of the scapula is attached the coracoid portion of the girdle. This is a plate of cartilage and bone lying on the under side of the body in the breast region and pierced by a wide oval space called the coracoid fontanelle. Behind the fontanelle lies the stout coracoid bone ; in front is a narrow strip of calcified cartilage, sometimes miscalled the precoracoid, continuous with another strip known as the epicoracoid which forms the inner border

of its half of the girdle and lies against its fellow in the middle line. These two are best called collectively the procoracoid. The junction of the two halves of the girdle is known as its symphysis. Scapula and coracoid are cartilage bones. A pair of slender membrane bones, the clavicles, overlie the precoracoid cartilages. Each sends forward a prolongation inside the acromion process. At the junction of the scapular and coracoid bones is the glenoid cavity, a hollow, lined by cartilage, on the hinder edge of the girdle, into which fits the head of the humerus or bone of the upper arm.

To the ends of the epicoracoids, before and behind the girdle,

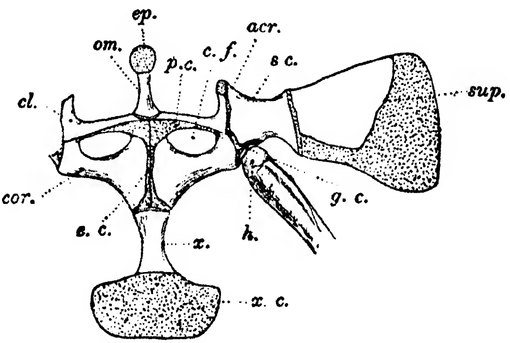


FIG. 22.13.—The shoulder girdle of a frog, seen from below, with the right scapula removed, and the left suprascapula bent ventralwards, so that it appears to lie in the same plane as the scapula.

acr., Acromion process; *c.f.*, coracoid fontanelle; *cl.*, clavicle; *cor.*, coracoid; *e.c.*, epicoracoid; *ep.*, episternum; *g.c.*, glenoid cavity; *h.*, head of humerus; *om.*, omosternum; *p.c.*, procoracoid; *sc.*, scapula; *sup.*, suprascapula; *x.*, xiphisternum; *x.c.*, xiphoid cartilage.

are attached certain structures which correspond to the breastbone or sternum of other animals. In front is a bone known as the omosternum, bearing at its end a small plate of cartilage, the episternum. Behind is the larger xiphisternum, bearing the broad, flat xiphoid cartilage.

The pelvic or hip girdle (Fig. 22.14) lies at the hinder end of the trunk in a position similar to that occupied in front by the shoulder girdle, which it also resembles in consisting of two halves, each composed of several pieces, joined below in a symphysis. Its shape, however, is very different ; it is connected with the backbone not solely by muscles, but also by joints or articulations with the large transverse processes of the sacral vertebra ; it bears no bone comparable with the clavicle and

there are in connection with it no unpaired structures like the sternum. The greater part of each half consists of a long slender bone, the hip-bone or ilium, corresponding in position to the scapular part of the shoulder girdle, which runs downwards and backwards from the sacral vertebra, curving inwards on the under side of the body to join its fellow. The junction is enlarged into a flattened mass by the addition of several elements which are more distinct while they are being formed in development

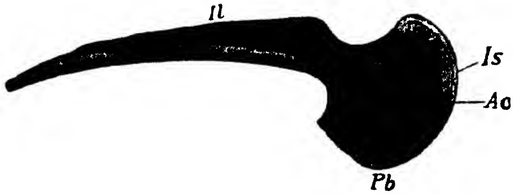


FIG. 22.14.—Side view of frog's pelvis.—From Thomson, after Ecker.

Ac., Acetabulum ; *Il.*, ilium ; *Is.*, ischium ; *Pb.*, pubis.

than they are in the adult. Behind lies a ridge of bone known as the ischium, which consists at first of two parts, one belonging to each half of the girdle. A slight groove marks the limits of this bone. Ventrally, between the ilium and the ischium, lies a triangular piece of calcified cartilage, the pubic cartilage. In each of the flat sides of the mass formed by the union of these structures is a round hollow, the leg-socket or acetabulum, into which fits the head of the thigh-bone.

LIMBS

The upper arm contains a single bone, the humerus. This consists of a stout shaft, swollen at each end, and bearing on its inner side a ridge known as the deltoid ridge. The swelling at the upper end is the head, and fits into the glenoid cavity of the shoulder girdle. That at the lower end, the trochlea, is more irregular in shape and serves for the articulation of the forearm bone or radio-ulna, which bears a groove showing its origin from two bones, an inner radius and an outer ulna. The upper end of the radio-ulna is hollowed to receive the humerus at the elbow-joint, behind which it projects as the elbow-bone or olecranon process. The wrist consists of six small carpal bones arranged in two rows across the limb. Those of the first row are named

according to their position, radiale, intermedium, and ulnare.[1] The second row contains in the early stages of its development five bones, called distal carpals, corresponding to five digits, but in the adult frog the third, fourth, and fifth of these have fused. The palm contains five metacarpal bones. The first digit is wanting, but the second and third have each two bones and the fourth and fifth three, according to the number of their joints. These bones are called phalanges (singular phalanx) and they may be represented by the conventional formula 02233.

The bones of the leg correspond closely to those of the arm. The thigh-bone or femur has a long, slender, slightly sigmoid shaft with a rounded head to fit into the acetabulum and a wide condyle for articulation with the shank-bone, or tibiofibula. The latter, like the radio-ulna, corresponds to two bones in man and many other animals, showing traces of being formed by the fusion of an inner or anterior shin-bone or tibia and an outer or posterior fibula. The ankle, like the wrist, consists of two rows of bones, which are here called tarsals. The first row contains two bones, the tibiale, and the heel-bone or fibulare.[1] These bones are joined at each end by a piece of cartilage. The second row consists of two small distal tarsals. The metatarsus contains six metatarsals, one minute and corresponding to a small extra toe, the prehallux or calcar, which lies inside the first toe or hallux, but does not project from the foot. The numbers of phalanges beginning with that for the calcar, which is put in brackets, are (1)22334.

LOCOMOTION

The arrangement of the chief muscles of the frog is shown in Figs. 22.15 and 22.16.

It would not be possible here to describe the various modes of locomotion of the frog, even if they were at present thoroughly understood. Something must, however, be said about crawling, in which the frog practises what is the primary mode of locomotion of four-footed animals. In it the body is levered forwards over the ground by the limbs, which are used in diagonal pairs, the left hind-limb immediately after, or practically with, the right fore-limb, and similarly the right hind-limb with the left fore-limb. Fig. 22.17 shows a toad moving in this way.

[1] For other names of the bones of wrist and ankle see p. 562.

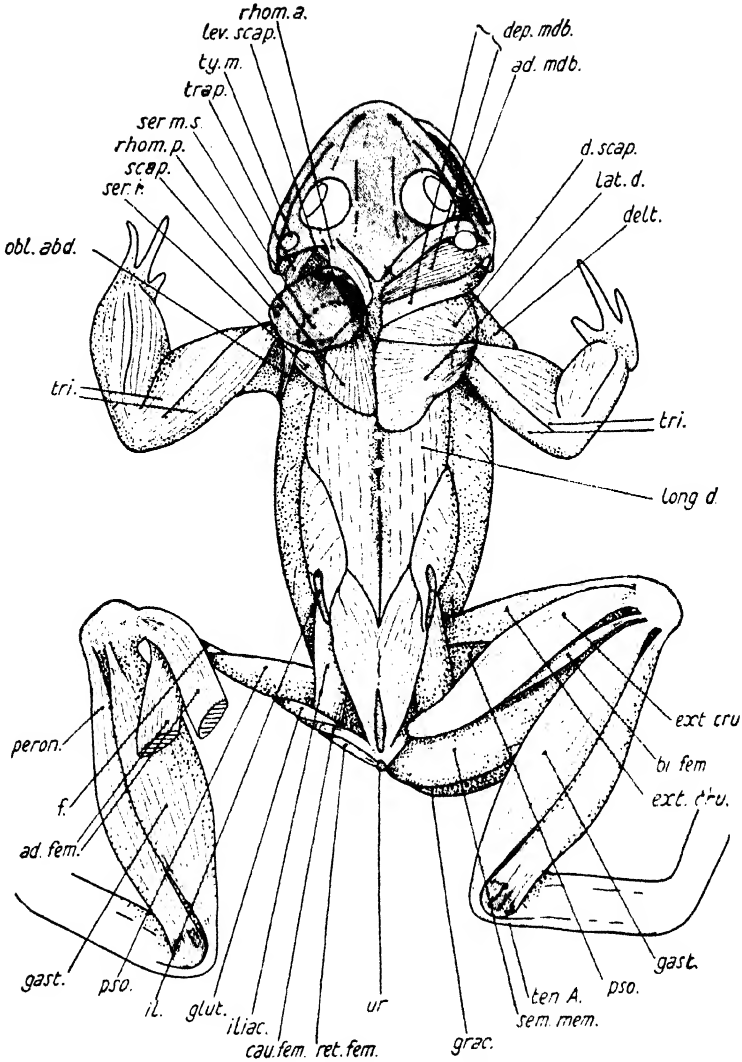


FIG. 22.15.—Dorsal view of skinned frog showing the superficial muscles on the right and the deeper muscles on the left; some connective tissue, and on the left the following muscles, have been removed: depressor mandibularis, adductor mandibulæ, dorsalis scapulæ, latissimus dorsi, deltoides, extensor cruris, biceps femoris, flexor cruris, part of adductor femoris. Exposed and nearly exposed bone and cartilage are shown by mechanical stippling.—From Saunders and Manton, *A Manual of Practical Vertebrate Morphology*, 2nd edition, 1949.

ad.fem., Adductor femoris; ***ad.mdb.***, adductor mandibulæ; ***bi.fem.***, biceps femoris; ***cau.fem.***, caudofemoralis; ***cor.br.***, coracobrachialis; ***d.scap.***, dorsalis scapulæ; ***delt.***, deltoideus; ***dep.mdb.***, depressor mandibularis; ***ext.cru.***, extensor cruris; ***f.***, femur; ***gast.***, gastrocnemius; ***gen.hy.***, geniohyoideus; ***gen.gl.***, genioglossus; ***glut.***, gluteus; ***grac.***, gracilis (part of flexor cruris); ***hum.cr.***, humeral crest (deltoid ridge); ***hy.gl.***, hyoglossus; ***il.***, ilium; ***iliac.***, iliacus; ***lat.d.***, latissimus dorsi; ***lev.scap.***, levator scapulæ; ***long.d.***,

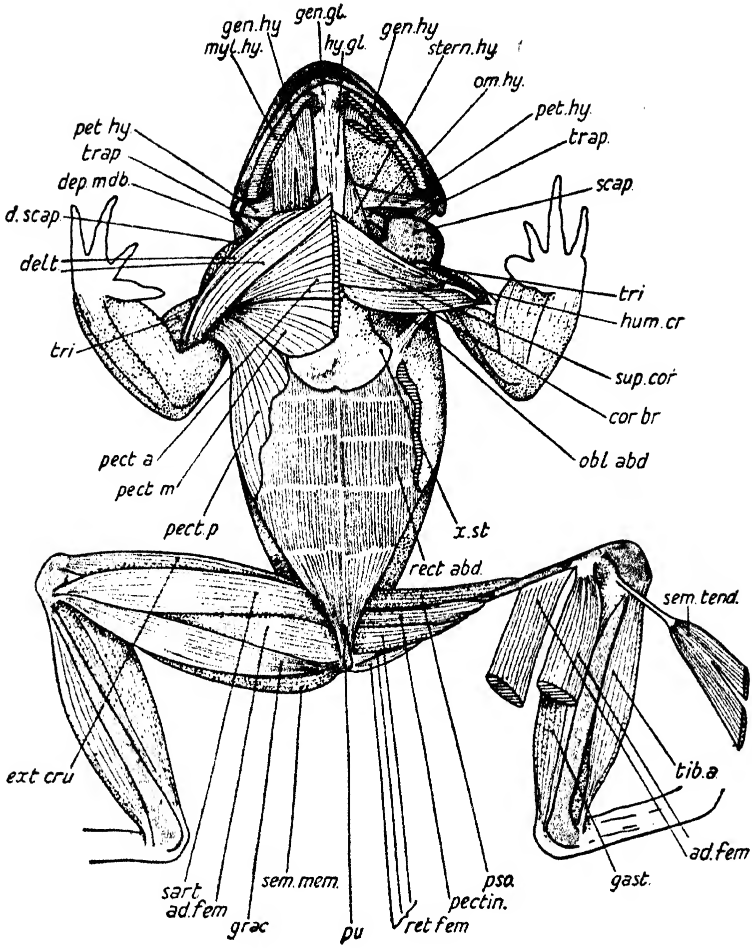


FIG. 22.16.—Ventral view of skinned frog showing superficial muscles on the animal's right and deeper muscles on the left. Some connective tissue and the mylohyoideus have been cut away on both sides, and on the left the following muscles have been removed wholly or in part: geniohyoideus; depressor mandibularis; deltoideus; dorsalis scapulæ; pectorales anterior medius and posterior; extensor cruris; sartorius; gracilis; semimembranosus. The adductor femoris and semitendinosus have been reflected. Exposed or nearly exposed bone and cartilage are shown by mechanical stippling.—From Saunders and Manton, *A Manual of Practical Vertebrate Morphology*, 2nd edition, 1949.

longissimus dorsi; *myl.hy.*, mylohyoideus; *obl.abd.*, obliquus abdominis; *om.hy.*, omohyoideus; *pect.a.*, pectoralis anterior; *pect.m.*, pectoralis medius; *pect.p.*, pectoralis posterior; *pectin.*, pectineus; *peron.*, peroneus; *pet.hy.*, petrohyoideus; *pso.*, psoas; *pu.*, pubes; *rect.abd.*, rectus abdominis; *ret.fem.*, retractor femoris; *rhom.a.*, rhomboideus anterior; *rhom.p.*, rhomboideus posterior; *sart.*, sartorius; *scap.*, suprascapula; *sem.mem.*, semimembranosus (part of flexor cruris); *sem.tend.*, semitendinosus (part of flexor cruris); *ser.i.*, serratus inferior; *ser.m.s.*, serratus medius and serratus superior seen, superimposed, through the transparent suprascapula; *stern.hy.*, sternohyoideus; *sup.cor.*, supracoracoideus; *ten.A.*, Achilles tendon; *tib.a.*, tibialis anticus; *trap.*, trapezius; *tri.*, triceps; *ty.m.*, tympanic membrane; *ur.*, urostyle; *x.st.*, xiphisternum.

FIG. 22.17.—(*From left to right*) Successive postures of a toad during crawling.—After Gray.

ALIMENTARY SYSTEM

The food of the frog is received and digested by a winding tube, known as the gut or alimentary canal, which runs from mouth to cloacal opening and has a muscular wall lined by a soft, glandular mucous membrane (p. 512). The gape of the mouth lies between two jaws, of which the upper is not movable, but the lower is hinged to the upper. There are no teeth in the lower jaw, but the upper bears a row of maxillary teeth, and a patch of vomerine teeth is found on each side of the roof of the mouth. The teeth are small and sharp-pointed with the usual structure, except that the root is formed of bone (Fig. 22.18). The teeth are all alike, and are fused to the surface of the bones that carry them. As they are destroyed by use they fall out and are replaced one by one. On the front part of the roof of the mouth, beside the vomerine teeth, open the internal nares. The tongue is a muscular structure arising, unlike that of man, from the front part of the floor of the mouth and forked at its free end, which is directed backwards when it is at rest. In taking food the tongue is turned over and its free end thrown out of the mouth, wiping up, as it goes, a sticky substance secreted by glands in the

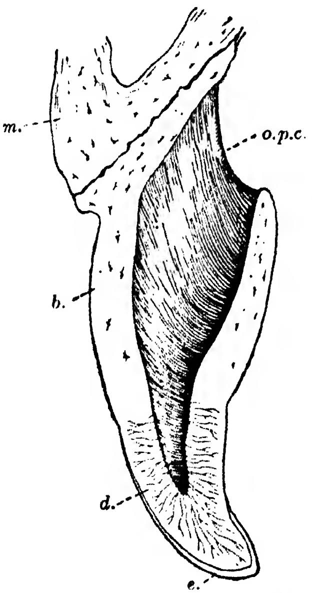


FIG. 22.18.—A vertical section through a tooth and part of the maxilla of a frog.

b, Base of the tooth, composed of bone; *d.*, dentine; *e.*, enamel; *m.*, maxilla; *o.p.c.*, opening of the pulp cavity.

roof of the mouth so that the prey adhere to it. The extrusion of the tongue is produced by the sudden passage into it of lymph, squeezed from one lymph sac to another by muscular contraction.

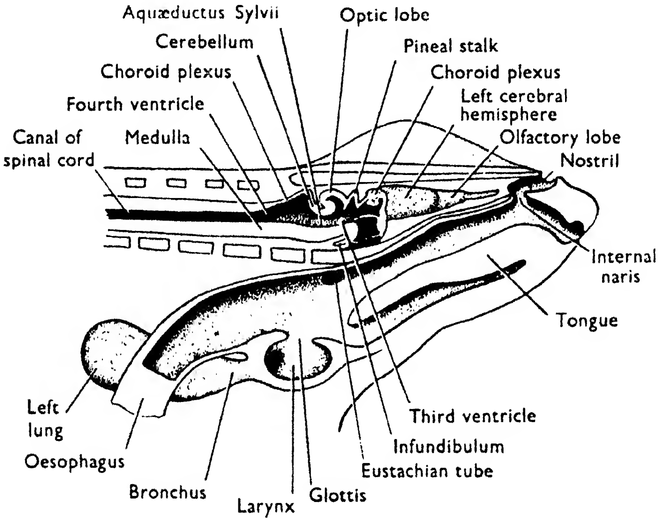


FIG. 22.19.—The head of a frog, cut sagittally and viewed from the right side

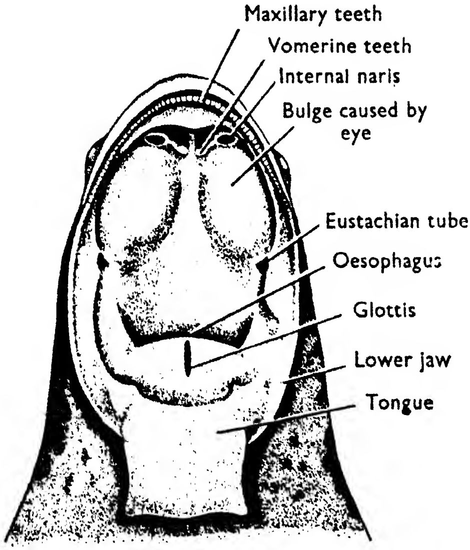


FIG. 22.20.—The mouth of a frog.

Behind the angle of the jaw is a region known as the pharynx, into which open, at the sides of its roof, the pair of Eustachian tubes

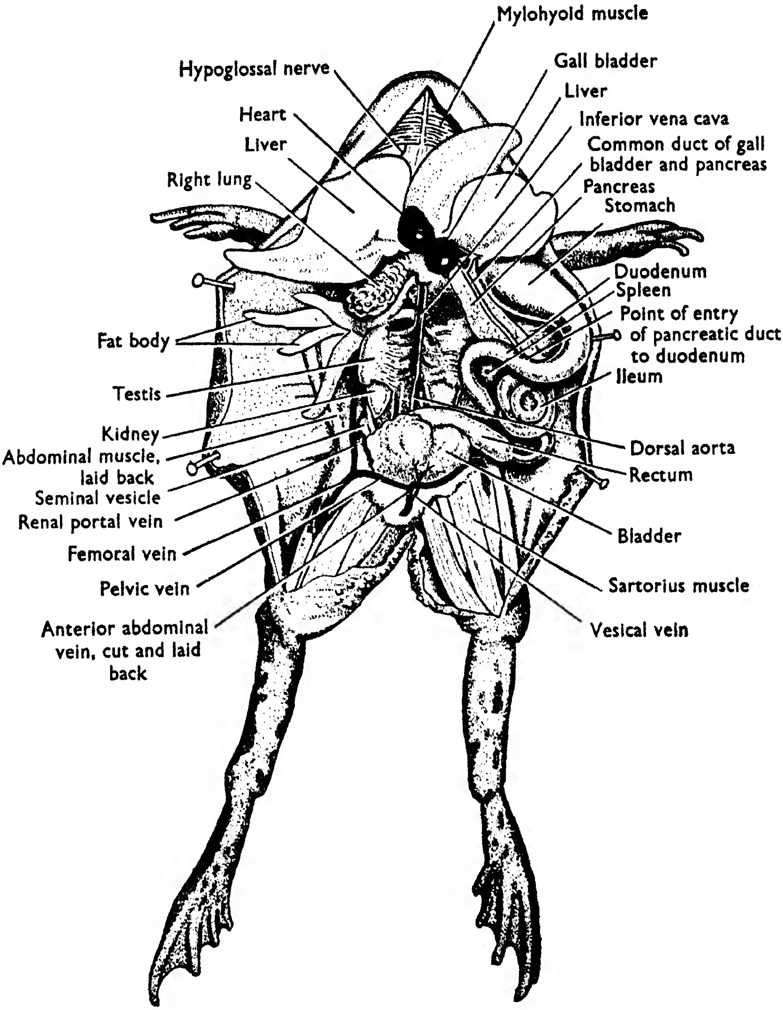


FIG. 22.21.—A male frog dissected from the ventral surface.

which lead to the drums of the ears, and below, in the male, a pair of vocal sacs which are inflated and act as resonators during croaking. In the middle of the floor of the pharynx is a slit-like opening, the glottis, which leads into the wind-pipe (Figs. 22.19 and 22.20).

From the pharynx a tube known as the gullet or œsophagus leads backwards in the body cavity to the stomach (Fig. 22.21), which is spindle-shaped and separated by a slight constriction, the pylorus, from the intestine. The first part of the intestine, known as the duodenum, is narrow and turns forward so as to lie parallel with the stomach. It is succeeded by another narrow tube, the ileum, which runs backwards in several coils. Duodenum and ileum are together known as the small intestine: at its hinder end this region opens suddenly into a much wider tube, the rectum. The length of the small intestine is from 4 to 5 inches; that of the rectum is about an inch and a quarter. The internal surface of the intestine is increased by folds of its lining. These are transverse in the duodenum and longitudinal in the ileum. The rectum passes without a distinct anus into a cloaca, which receives ventrally a thin walled, bilobed sac, the urinary bladder, and dorsally the ducts of the kidneys and in the female those which bear the eggs.

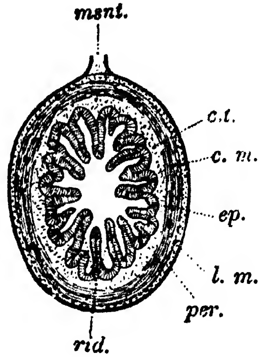


FIG. 22.22.—A diagram of a transverse section through the ileum of the frog.

c.m., Circular muscle layer; *c.t.*, connective tissue; *ep.*, epithelium which lines the gut; *l.m.*, longitudinal muscle layer; *msnt.*, mesentery; *per.*, peritoneum; *rid.*, longitudinal ridges of ileum.

Besides numerous small glands in the mucous membrane, the alimentary canal receives the secretions of two large glands, the liver and the pancreas. The liver is a large, reddish-brown structure in the forepart of the belly. It consists of a right and a left lobe and a small median lobe which unites them. The left lobe is the larger and is itself deeply cleft into two. Between the right and left lobes lies the gall-bladder, which receives the green bile secreted by the liver and passes it by the bile-duct into the duodenum. The pancreas is an oblong, creamy-white structure lying between the stomach and duodenum. It is traversed by the bile-duct, into which it passes the pancreatic juice which it secretes.

DIGESTION

The food is not chewed, but is swallowed whole, the only use of the teeth being to prevent the escape of the prey, which they can the better do because they slant backwards. Digestion follows the same general course as in the mammal (p. 440). Pepsin, however, is produced by the œsophagus as well as by the

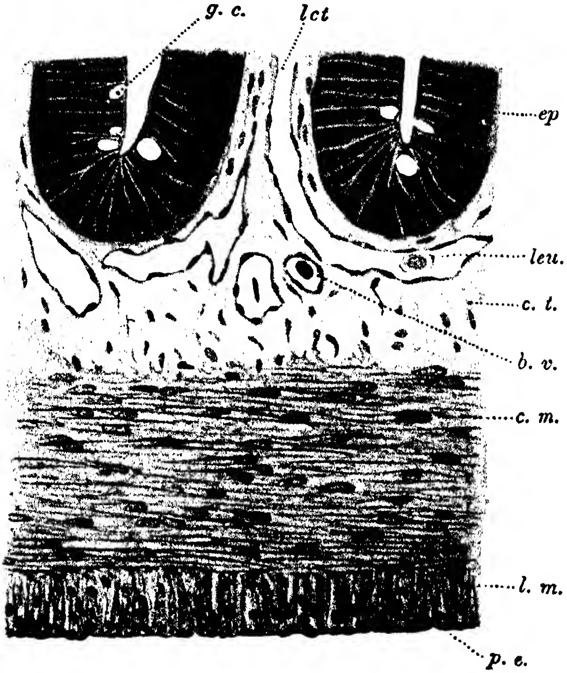


FIG. 22.23.—A portion of the section shown in Fig. 22.22, more highly magnified. *b.v.*, Blood vessel; *c.t.*, connective tissue of mucous membrane; *c.m.*, circular layer of muscle fibres; *ep.*, epithelium; *g.c.*, goblet cell; *lct.*, 'lacteal' or lymph vessel of the intestine; *leu.*, leucocyte of lymph or lymph corpuscle; *l.m.*, longitudinal layer of muscle fibres; *p.e.*, peritoneal epithelium.

stomach, the secretion of which is not so acid as in man; in it the food remains for from one to three days.

ENDOCRINE AND OTHER ORGANS

The endocrine glands are similar, in general structure and function, to those of the mammal, but their hormones have some special functions.

The thyroid glands are a pair of small, rounded, pinkish bodies

lying on the external jugular veins. Their secretion brings about the change from tadpole to adult (Fig. 22.24).

The thymus is a small body which lies behind and above the angle of the jaw on each side.

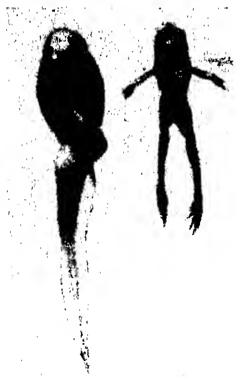


FIG. 22.24.—Two individuals of the same age from the same batch of frog's eggs. The one on the right has changed normally into a frog; that on the left had the rudiment of its thyroid removed and has not become adult but has grown into a giant tadpole.—From Haldane and Huxley.

FIG. 22.25.—Two frogs nineteen days after operation. From that on the left only the anterior lobe of the pituitary body has been removed; from that on the right both anterior and posterior lobes. Lack of the hormone from the posterior lobe has caused in the right-hand frog pallor due to non-expansion of the pigment in the pigment cells.—From Hogben.

The pituitary body lies in the skull below the brain (see p. 470) (Fig. 22.25) Two hormones from the posterior lobe control the dispersion and concentration of the pigment in the melanophores of the skin, so causing changes in colour.

The adrenal bodies (so-called suprarenal glands) are small yellowish masses lying on the ventral face of the kidneys. They consist of two kinds of tissue, which in the frog are mixed, while in man one, the cortex, is a layer around the other, the medulla.

The spleen is a small, round, dark red body, lying in the mesentery opposite to the beginning of the rectum.

The fat bodies are two orange-coloured tufts of flattened processes, attached in front of the ovary or testis to the dorsal wall of the body cavity. They consist of fatty tissue (see p. 519) which, like the reserves in the liver, increases during the summer and decreases during the winter sleep, when it is being drawn upon for nourishment, particularly in the preparation of germ cells for breeding in the spring.

VASCULAR SYSTEM: HEART

The heart of the frog (Figs. 22.26, 22.27), is a hollow, conical, muscular organ, which lies, with the apex pointing backwards, in the body cavity, between the breast-bone and the gullet. It is enclosed in a thin sac, the pericardium, whose cavity is a part of the body cavity (cœlom) separated from the rest during development, the heart having the same relation to it that the alimentary canal has to the pleuroperitoneal or general body cavity—that is, being covered by a continuation of the pericardial membrane as the gut is by the peritoneum. The heart contains five chambers. Of these the most conspicuous is the ventricle, a large, conical structure, with thick, muscular walls, with projections called columnæ carneæ; from it arises in front, on the right side of the ventral surface, the much smaller tubular truncus arteriosus. The right and left auricles or atria are relatively thin-walled chambers, the right larger than the left, separated by a septum and lying in front of the ventricle, into which each opens. On the dorsal surface of the heart, opening into the right auricle, lies the still thinner-walled, triangular sinus venosus; into the left auricle opens the pulmonary vein (p. 371).

The openings between these chambers are guarded by certain valves or folds of the lining of the heart. Two simple lips of the opening between the sinus and right auricle are the sinu-auricular

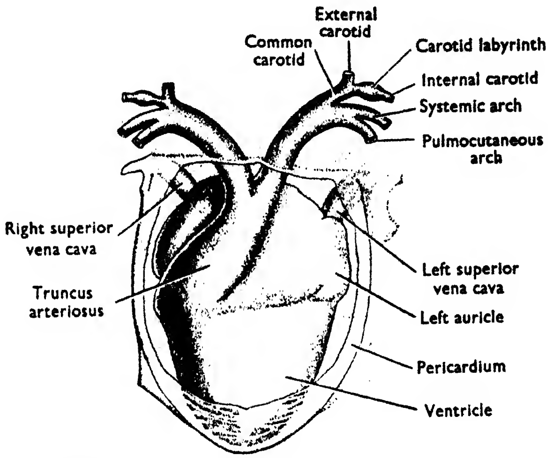


FIG. 22.26.—The heart of a frog from the ventral surface. The wall of the pericardium has been cut open.

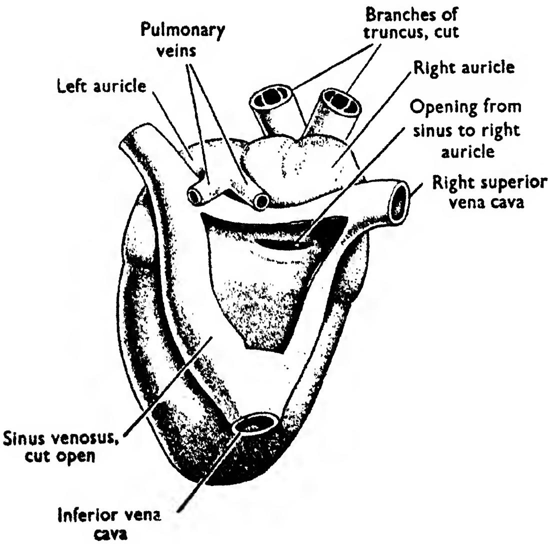


FIG. 22.27.—The heart of a frog from the dorsal surface. The pericardium has been removed and the sinus venosus cut open.

valves; these allow blood to flow into the auricle, but when it tends to flow the other way fold over and meet to oppose it. The edge of the auricular septum is cleft and projects into the ventricle as two flaps, the auriculo-ventricular valves. Each of these is connected with the walls of the ventricle by fine cords, the chordæ tendineæ, and thus, while blood can pass from auricles to ventricle, its reflux is prevented by its raising the valves, which are kept from turning back into the auricle by the chordæ tendineæ. The opening from ventricle to truncus is guarded by three semilunar valves, shaped like watch-pockets, which are spread out by any reflux of blood, so that by meeting one another they stop it. The truncus arteriosus is divided internally by a second ring of semilunar valves into two unequal parts, a long conus arteriosus next the ventricle, and a short ventral aorta. The conus is incompletely divided longitudinally by a spiral valve into an aortic part, which begins dorsally and curves round by the right to become ventral, and a pulmocutaneous part, which begins ventrally and curves round by the left to become dorsal. The ventral aorta is completely divided into a dorsal and a ventral chamber by a septum which ends towards the heart by cutting across the hollow of one of the second row of semilunar valves. It is from the outer side of this valve that the spiral valve starts. Thus it comes about that the outer ends of the two parts of the

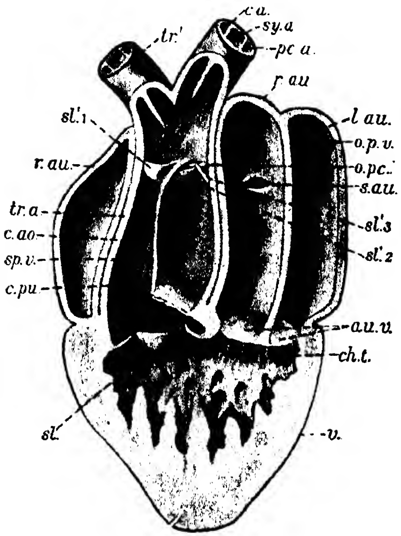


FIG. 22.28.—A ventral view of the heart of a frog, opened to show the internal structure. The ventral wall of the truncus, ventricle, and auricles has been removed, with part of the spiral valve.

au.v., Auriculo-ventricular valves; *c.a.*, carotid arch; *c.ao.*, cavum aorticum; *c.pu.*, cavum pulmocutaneum; *ch.t.*, chordæ tendineæ; *l.au.*, left auricle; *o.p.v.*, opening of pulmonary vein; *o.pc.*, opening of dorsal division of the aorta; *pc.a.*, pulmocutaneous arch; *r.au.*, right auricle; *s.au.*, sinu-auricular opening with valves; *sl.*, first row of semilunar valves; *sl'.1*, the semilunar valve from which the spiral valve starts; *sl'.2*, small semilunar valve at end of cavum pulmocutaneum; *sl'.3*, a small part of a large semilunar valve, of which the rest extends across that portion of the front wall of the truncus which has been removed; *sp.v.*, spiral valve; *sy.a.*, systemic arch; *tr.a.*, wall of truncus arteriosus; *tr'.*, one of the two bundles of arteries into which the truncus divides; *v.*, ventricle.

conus are each guarded by one and a half valves. The dorsal chamber of the aorta communicates behind with the pulmocutaneous part of the conus and in front with the blood vessel to the lungs (pulmocutaneous arch) ; the ventral chamber communicates behind with the aortic part and in front with the blood vessels known as the systemic and carotid arches.

HEART-BEAT

The contraction starts in the sinus venosus, driving the contained blood into the right auricle. Meanwhile the left auricle is filling by the inflow of blood from the lungs through the pulmonary vein. The auricles now contract simultaneously, driving the blood into the ventricle. The sinus is beginning to relax, but the reflux of blood into it is prevented by the sinu-auricular valves. The right-hand side of the ventricle receives the blood from the right auricle and the left-hand side that from the left auricle, but these portions of blood mix rapidly so that there is not, as is generally imagined, any further separation of the two streams. The ventricle contracts immediately after the auricles, the auriculo-ventricular valves preventing the passage of blood back into the latter. The effect of the contraction of the ventricle is therefore to drive the blood onward into the truncus arteriosus. Both parts of this are filled, and the blood flows into the carotid, systemic, and pulmocutaneous arches nearly, if not quite, simultaneously. The heart of the frog, with its single ventricle, is perhaps not primitive, and the muscles of the wall seem to get most of their oxygen from the blood in the chambers, since the single coronary artery is small.

BLOOD VESSELS

From the truncus arteriosus there arise on each side three arteries, which are for some distance bound together, so that they seem to be a single vessel. The hindermost of these is the pulmocutaneous arch, the middle the systemic arch, the foremost the carotid arch or common carotid artery. After separating, the three arches continue to run outwards, diverging as they go. The pulmocutaneous arch divides into the pulmonary artery for the lung and the cutaneous artery for the skin and mouth. The carotid arch gives a lingual or external carotid artery to

the muscles of the tongue and hyoid, and then becomes the internal carotid artery which bears a round swelling due to the fact that it here breaks up into a number of small vessels which reunite. This swelling is the carotid labyrinth, often inappropriately called the carotid gland. The friction of the blood against the large surface provided by its numerous small vessels is the

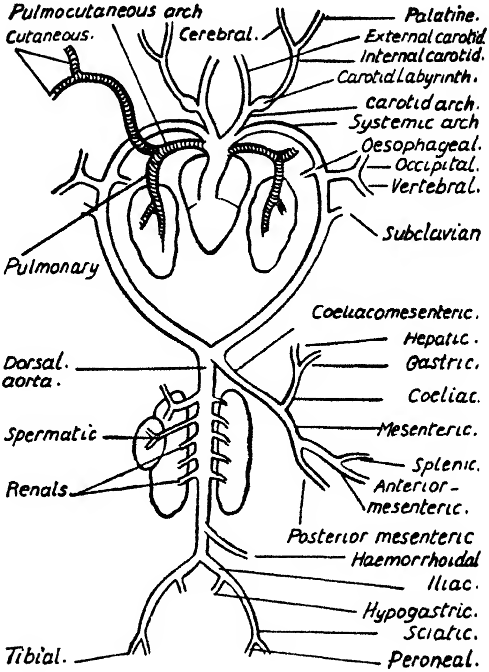


FIG. 22.29.—A diagram of the arterial system of the frog, seen from the ventral side.

cause of the high pressure in the carotid arch. Beyond the carotid labyrinth the artery runs forwards and upwards towards the head, where, after an orbital (stapedial) branch to the orbit and roof of the mouth, it passes into the skull and supplies the brain. The systemic arch curves upwards and backwards round the œsophagus to join its fellow in the middle line below the backbone. On its way it gives off an œsophageal artery to the œsophagus, an occipitovertebral artery to the head and backbone, and a large subclavian artery to the arm. Just before joining its fellow, the left systemic arch gives off backwards the large cœliacomesenteric artery. This divides into an anterior mesenteric, to

bowel and spleen, and a cœliac, which supplies the stomach after giving a hepatic branch to the liver. The vessel formed by the junction of the systemic arches is the dorsal aorta. It runs backwards immediately below the backbone, giving off paired renal arteries to the kidneys, ovarian or spermatic arteries to

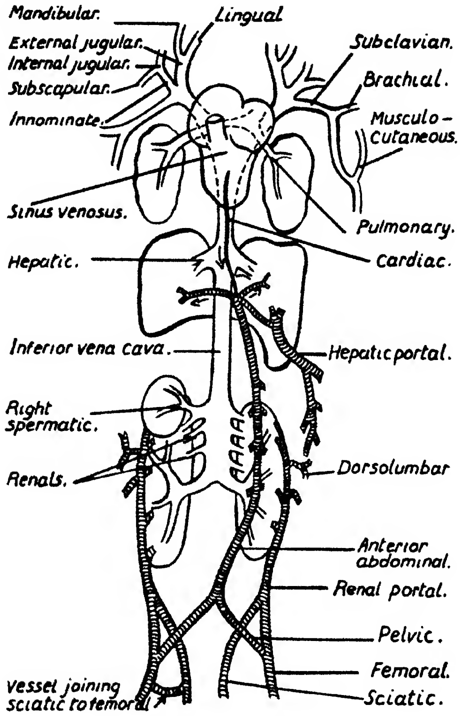


FIG. 22.30.—A diagram of the venous system of the frog.

the generative organs, and a small median posterior mesenteric artery to the rectum, after which it divides into two iliac arteries to the legs and abdominal muscles.

The blood from the lungs is returned by the right and left pulmonary veins, through a short common pulmonary vein to the left auricle. From the rest of the body the blood is returned to the sinus venosus by three large veins, the right and left superior or anterior venæ cavæ or precaval veins in front, and the median inferior or posterior vena cava or postcaval vein

behind. Each precaval is formed by the junction of three veins, the external jugular, innominate, and subclavian. The external jugular is fed by a lingual vein from the floor of the mouth and a mandibular from the lower jaw. The innominate arises by the junction of an internal jugular from the head and a subscapular from the shoulder and back of the arm. The subclavian receives the brachial from the arm and the great musculocutaneous from the skin, the mucous membrane of the mouth, and many head and trunk muscles. The inferior vena cava arises by the junction of several renal veins from the kidneys and ovarian or spermatic veins from the generative organs, and, just before it enters the sinus, is joined by two hepatic veins from the liver. Blood is returned from the legs by a femoral vein on the outside and a sciatic on the inside of each limb. Each femoral vein divides on reaching the trunk into a renal portal and a pelvic. The former receives the sciatic and runs to the kidney, just before entering which it receives the dorsolumbar vein from some of the muscles of the back. In the kidney the vein breaks up into capillaries, which are collected, with those of the renal artery, to give rise to the renal veins. Thus it comes about that much of the blood in the renal veins has passed through two sets of capillaries, one in the leg and another in the kidney. Such an arrangement, in which the blood having passed through one set of capillaries is then sent through a second, is called a portal system. The pelvic veins of the two sides lie in the abdominal wall and join to form the central abdominal vein which runs forwards above the linea alba in the middle of the belly. This vessel receives a small vesical vein from the bladder, several pairs of vessels from the muscles of the abdomen, and a little backward vessel from the heart wall. It ends in front by passing into the liver and there breaking up into capillaries again. The blood from the stomach, bowel, pancreas, and spleen is gathered up into a great hepatic portal vein, which also breaks up in the liver. Thus the liver has a portal system, which is fed both from the central abdominal vein and from

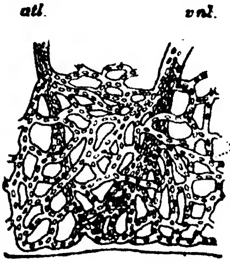


FIG. 22.31.—Capillaries in the web of a frog's foot.—After Allen Thomson.

atl., Arteriole; *cap.*, capillaries; *vnl.*, venule.

the hepatic portal vein, and discharges by the hepatic veins into the inferior vena cava.

Abnormalities in the vascular system, such as the absence of

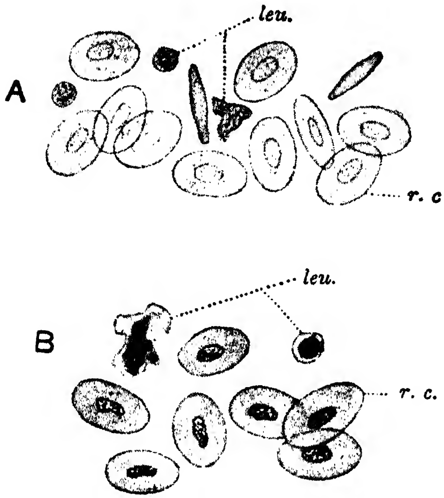


FIG. 22.32.—Blood of a frog, highly magnified.

A, Fresh ; *B*, stained.

leu., Leucocytes ; *r.c.*, red corpuscles.

the precaval of one side and its replacement by a transverse connection to that of the other side, are common.

The capillaries of the frog are well seen in the web of the foot (Fig. 22.31).

The red cells in the blood (Fig. 22.32) are biconvex, oval and nucleated and much larger than those of mammals ; they are mostly formed in the kidney and destroyed in the spleen and liver. There are the usual three types of white cell : lymphocytes, monocytes, and polymorphonuclears.

LYMPH

The lymph that escapes from the blood vessels is gathered by small lymphatic vessels into the big lymph sacs already mentioned, whence it is pumped back into the veins by two pairs of small contractile sacs known as lymph hearts. One pair of these lies below the scapulæ and opens into the subscapular veins ; the

other lies at the end of the urostyle and opens into the femoral veins. The fluids in the cœlomic (pleuroperitoneal and pericardial) cavities are lymph. The pleuroperitoneal cavity communicates with the dorsal lymph sacs by minute openings in the membrane which separates it from them.

ORGANS OF RESPIRATION

The respiratory organs of the frog are the lungs, the skin, and the mucous membrane of the mouth. The lungs communicate with the pharynx by way of the glottis, which leads into a short, wide windpipe consisting of the larynx or voice organ only, without the long trachea, or windpipe proper, which is found in animals with necks. The walls of this cavity are supported by a pair of flat arytenoid cartilages and a very irregular ring, the cricoid cartilage. The lining of the larynx is thrown into a pair of folds, the vocal cords. Between these is a narrow slit, the rima glottidis, through which the air must pass on its way to and from the lungs. The cartilages are supplied with muscles, by which they can be moved, so as to tighten the vocal cords and bring them close together. In this condition the cords vibrate when air from the lungs is forced between them, and produce a sound which is the croaking of the frog. From the hinder part of the windpipe an opening leads on each side to a short tube known as the bronchus, which begins at once to expand into the lung. The latter is a wide, thin-walled, elastic, highly vascular sac, whose internal surface is increased by numerous folds.

The lungs of the frog are not enclosed, like those of man, in a 'chest' shut off by a midriff, but lie free in the forepart of the common body cavity, and the mode of breathing (air renewal) is correspondingly different in the two cases. In man, as in the rabbit (p. 444), it consists in an enlargement of the chest, which draws air into it, followed by a collapse which drives it out. In the frog, air is pumped into the lungs by the mouth, the jaws being closed throughout the whole cycle. The buccal floor is lowered by muscles of the hyoid, and air is drawn in through the open nostrils ; the external nares are closed, and the raising of the buccal floor by the mylohyoid and jaw muscles forces air into the lungs, which have emptied by collapse of their elastic walls and pressure from abdominal muscles. The air forced into the lungs must be a mixture of that just expelled from them with fresh air

from outside. When the frog is at rest the lungs are only filled about once a minute, though the beat of the buccal floor is more rapid, and most of the necessary oxygen is taken up through the skin and the mucous membrane of the mouth. During hibernation the skin alone is used.

EXCRETORY ORGANS

The respiratory organs are engaged, as we have seen, in ridding the body of carbon dioxide, and some water is also lost in the form of vapour through these organs. A further loss of water in

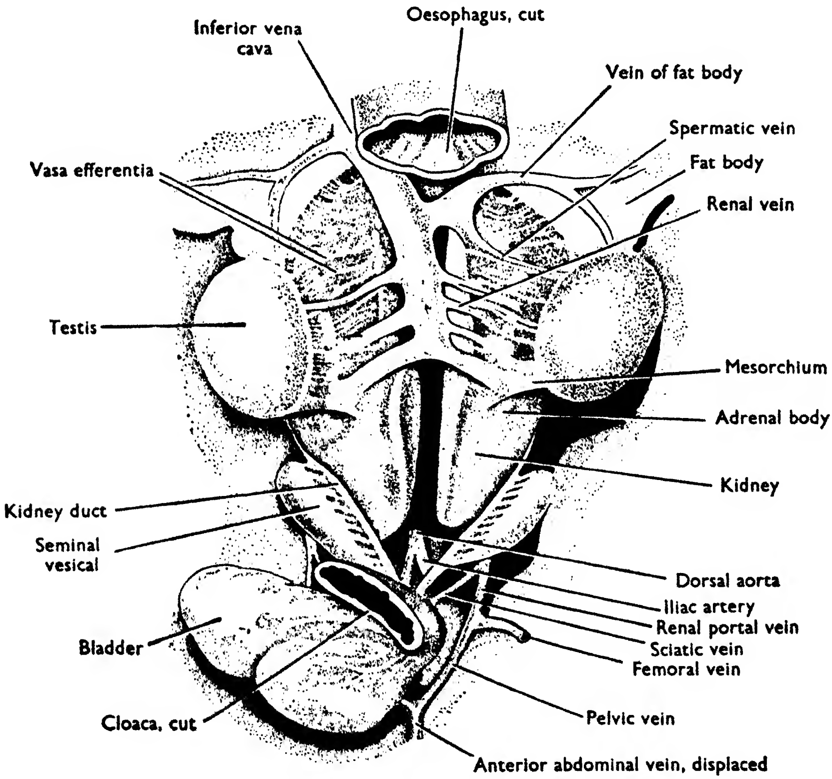


FIG. 22.33.—The urogenital organs of a male frog, dissected from the ventral surface. × 3.

a liquid form and the excretion of solids dissolved in it takes place through the kidneys (Figs. 22.33–22.36). These are a pair of flattened, oblong, dark-red bodies which lie one on each side in

the dorsal lymph sac above the cœlom and below the backbone. Their general structure and mode of action are similar to those of the rabbit (p. 453), but the tubules have an additional blood supply from the renal portal vein. The main duct, the Wolffian duct, which lies along the outer edge of the organ and passes backward to open into the dorsal side of the cloaca, should not be called the ureter since it does not correspond to that tube in mammals. The bladder, in which urine is stored, is a thin-walled diverticulum of the cloaca.

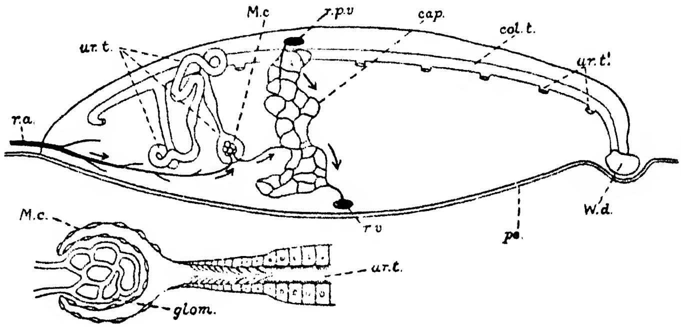


FIG. 22.34.—A diagram of a kidney of the frog, to show the arrangement of the tubules and blood vessels. One uriniferous tubule and a portion of the vascular meshwork are shown separately. In reality the blood vessels entangle the tubules.

cap., Capillaries; *col.t.*, collecting tubule; *glom.*, glomerulus; *M.c.*, Bowman's capsule; *pe.*, peritoneum; *r.a.*, renal artery; *r.p.v.*, branch of the renal portal vein; *r.v.*, branch of a renal vein; *ur.t.*, uriniferous tubule (somewhat unravelled; note that its regions differ); *ur.t'.*, places where other uriniferous tubules open into the collecting duct; *W.d.*, Wolffian or kidney duct.

ORGANS OF REPRODUCTION

The male organs of reproduction of the frog are the testes and their ducts. The testes are a pair of ovoid bodies slung from the surface of the kidneys by a fold of the peritoneum known as the mesorchium. Each consists of a mass of seminiferous tubules, in which the spermatozoa are formed. They communicate by about a dozen small ducts, the vasa efferentia, in the mesorchium, with the collecting tubules of the kidney, along which, and through the Wolffian duct, the sperms pass to the cloaca, for the male frog has not separate ducts for semen and for urine, but passes these fluids to the exterior through the same passage. Each Wolffian duct has attached to it a sac, the seminal vesicle, in which the sperms are stored until they are used for fertilising the eggs of the female. In the female, the ovaries correspond in

position to the testes, the membrane by which each of them is slung being known as the mesovarium. They are pleated folds of peritoneum containing ova in various stages of ripeness, each

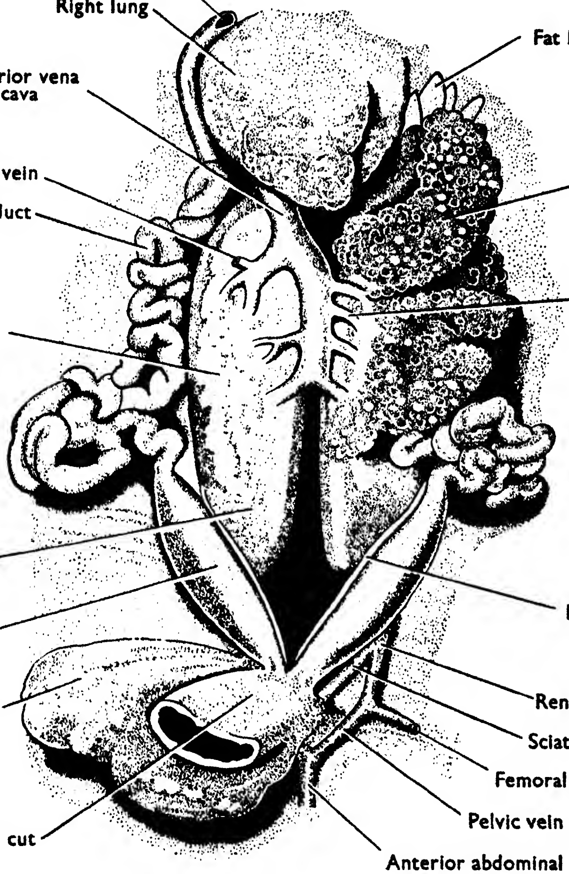


FIG. 22.35.—The urogenital organs of a female frog, dissected from the ventral surface. × 3.

ovum enclosed in a follicle of smaller cells and all held together by connective tissue. In the breeding season they enlarge and shed the ripe ova into the body cavity, where, by ciliary action, the ova are carried into the internal openings of the oviducts. These are long twisted tubes, one on each side of the body, opening in front into the body cavity by a small aperture at the

base of the lung, and behind into the cloaca just before the opening of the Wolffian duct. The greater part of each tube is narrow and glandular and secretes a slimy substance, but at its hinder end the duct enlarges into a sac, which at the breeding season becomes distended with eggs and occupies a greater part of the body cavity. At this season, which is in March, frogs return in large numbers to the ponds where they were hatched. The male recognises a gravid female by her size and warty skin and mounts upon her back, clasping her behind the arms with his fore-limbs, which are

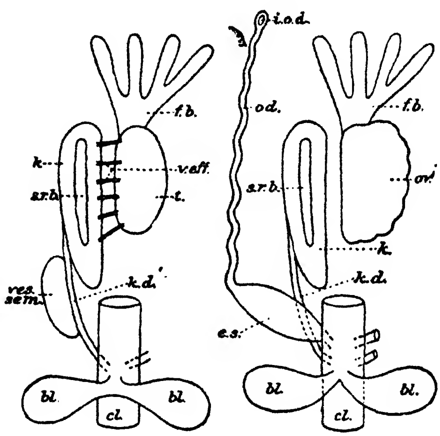


FIG. 22.36.—Diagrams of the urinary and generative organs of the frog.

A, Organs of the male ; *B*, those of the female ; *bl.*, bladder ; *cl.*, cloaca ; *e.s.*, egg sac ; *f.b.*, fat body ; *i.o.d.*, internal opening of oviduct ; *k.*, kidney ; *k.d.*, kidney duct (Wolffian duct) ; *od.* oviduct ; *ov'.*, ovary ; *sr.b.*, adrenal body ; *t.*, testis ; *v.eff.*, vasa efferentia ; *ves.sem.*, vesicula seminalis.

provided for the purpose with the pads we have already mentioned. In this sexual embrace, called amplexus, the animals remain for days until the eggs are laid. As the spawn passes out, its contact with the pelvic region of the male acts as a stimulus for him to shed his sperms over it, the eggs are fertilised (p. 5), and the slimy coating that each of them has acquired in the oviduct swells up and sets in the water so as to form a layer of jelly. This is probably protective, since carnivorous triclads (p. 129) can only reach the eggs to feed on them if their probosces are long enough. With their subsequent history we shall deal later (p. 649). When the eggs have been laid the female croaks and this, with her reduced size, makes the male let go ; by this croaking he is also warned off if he tries to mount a female who

has laid her eggs, or another male. The males remain at the breeding pond for some weeks, and while some enter into amplexus with several females, others get none.

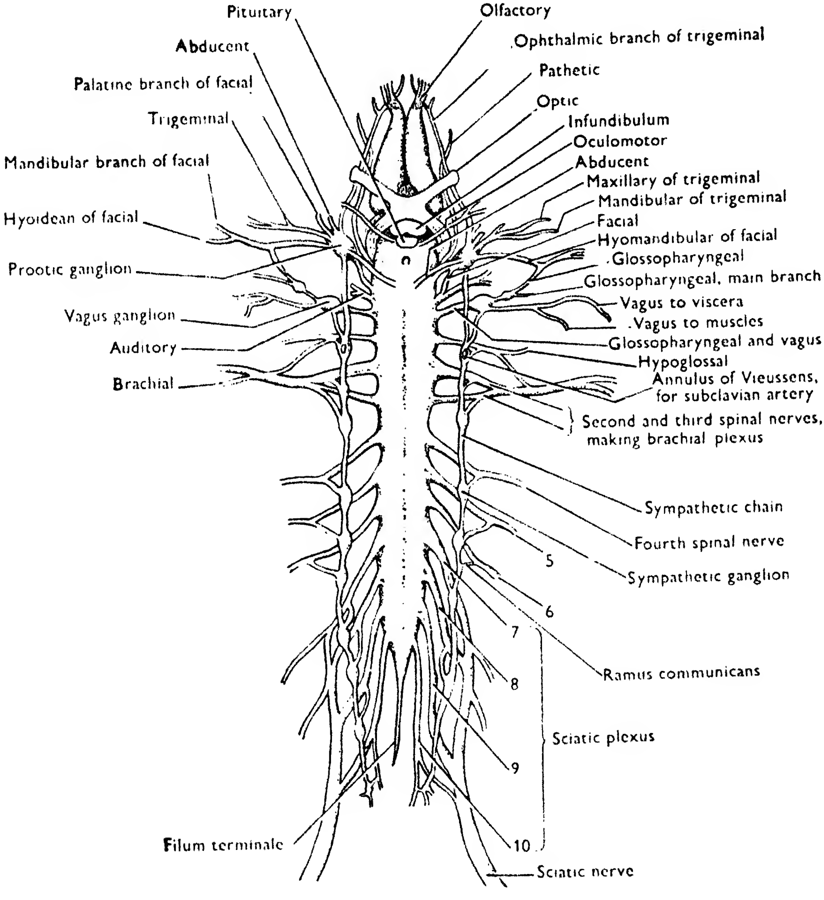


FIG. 22.37.—The central nervous system and principal nerves of a frog, seen from below. × 2.—Partly after Ecker.

The tadpole into which the egg hatches is a true larva (p. 244), swimming by a tail and breathing by gills. It feeds mainly on small particles which are entangled in mucus and carried along by cilia, in the same way as the food of *Branchiostoma* (p. 303). Some of these particles are rubbed off plants by a buccal rasp in the mouth, and larger particles, such as water-fleas and insect

larvæ, are also swallowed. Gradually it changes, losing its gills and tail and gaining lungs and two pairs of limbs, till at the end of three months it becomes a small frog.

SPINAL CORD

The spinal cord (Fig. 22.37) is an elongated, subcylindrical structure, lying in the vertebral canal. It is somewhat flattened from above downwards, tapers to a fine thread, the filum terminale, in the urostyle, and swells somewhat in the regions of the limbs. A transverse section (Fig. 26.25) shows that it is composed of nervous tissue of two kinds, a grey matter inside and a white matter outside (p. 539), enclosed in a connective tissue sheath, the pia mater, which along the dorsal and ventral middle lines passes in to some depth as the dorsal and ventral fissures. In the section the grey matter extends as dorsal and ventral horns on each side. In the grey matter is a longitudinal central canal, which ends blindly behind, but in front is continuous with cavities in the brain.

SPINAL NERVES

The ten pairs of spinal nerves pass out between the vertebræ to be distributed over the body. Each nerve is surrounded at its origin by a soft, white, calcareous concretion. Every nerve

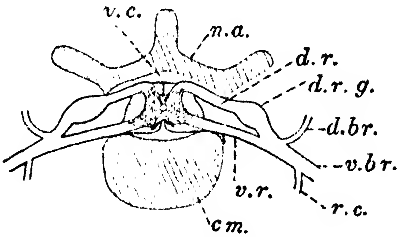


FIG. 22.38.—A diagram of the origin of the spinal nerves of the frog.

cm., Centrum ; *d.br.*, dorsal branch of the nerve ; *d.r.*, dorsal root ; *d.r.g.*, dorsal root ganglion ; *n.a.*, neural arch ; *r.c.*, ramus communicans ; *v.br.*, ventral branch *v.c.*, vertebral canal ; *v.r.*, ventral root.

arises by two roots, a dorsal and a ventral (Fig. 22.38), and the dorsal root bears a small swelling, the dorsal root ganglion. Just outside the backbone the two roots join, and the nerve thus formed proceeds at once to divide, giving rise to : (1) a short dorsal branch to the muscles and skin of the back, (2) a long

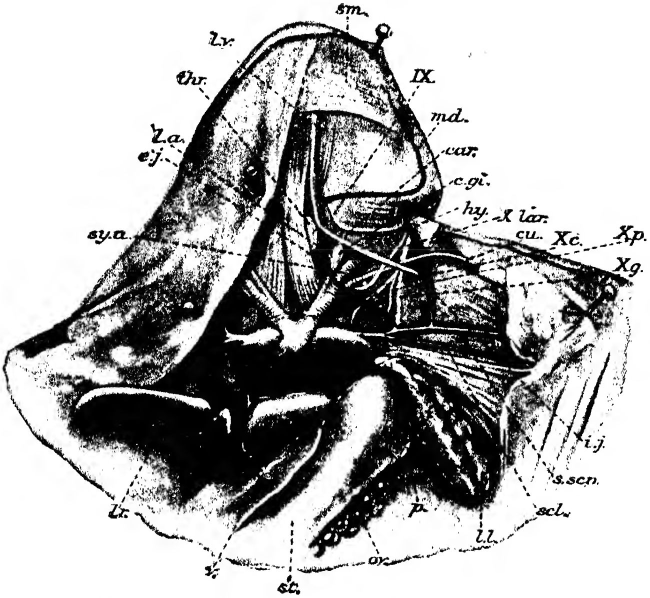


FIG. 22.39.—The forepart of a frog's body dissected from the ventral side, and stretched to display the organs.

., Carotid gland ; *car.*, common carotid artery ; *cu.*, cutaneous artery ; *e.j.*, external jugular vein ; *hy.*, hypoglossal nerve ; *i.j.*, internal jugular vein ; *l.a.*, lingual artery ; *l.l.*, left lung ; *l.v.*, lingual vein ; *lr.*, liver ; *md.*, mandibular vein ; *or.*, part of ovary ; *p.*, pulmonary artery ; *s.scp.*, subscapular vein ; *scl.*, subclavian vein ; *sm.*, submaxillaris or mylohyoid muscle ; *st.*, stomach ; *sy.a.*, systemic arch ; *thr.*, thyroid gland ; *v.*, ventricle ; *IX.*, glossopharyngeal nerve ; *Xc.*, *Xg.*, *Xlar.* *Xp.*, cardiac, gastric, laryngeal, and pulmonary branches of vagus nerve.

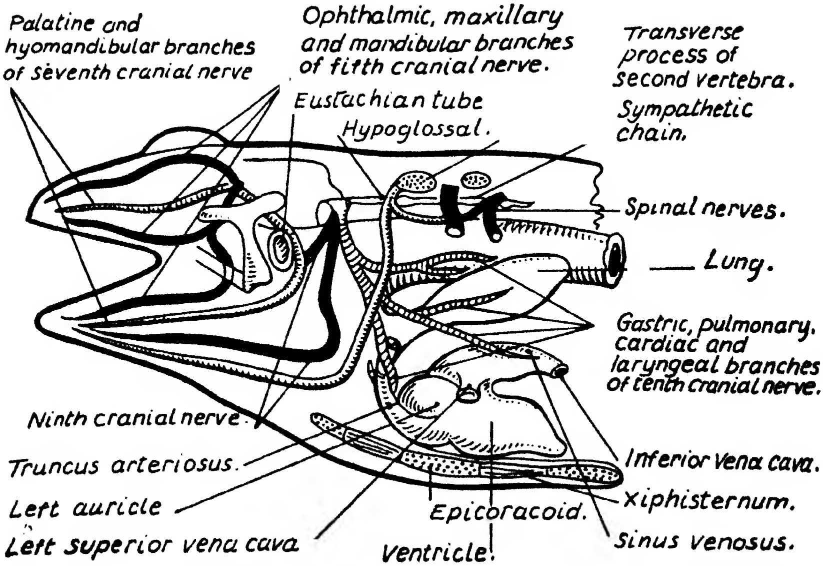


FIG. 22.40. A diagram of a dissection, from the left side, of the forepart of the body of a frog. Compare Fig. 22.39.

and conspicuous ventral branch to the muscles and skin of the sides and ventral surface of the trunk, and in some cases to the limbs, and (3) a small ramus communicans to the sympathetic system. The dorsal root is also called afferent or sensory because impulses pass inwards along it to the spinal cord and produce, among other effects, sensation; the ventral is called similarly efferent or motor because impulses pass outward along it and produce, among other effects, contraction of muscles and thus movements. These functions are proved by the fact that cutting the dorsal root deprives the parts supplied by its nerve of the power to send impulses to the central nervous system, while cutting the ventral root paralyses the same parts. Each of the branches contains elements derived from both dorsal and ventral roots. The course of the dorsal branches and rami communicantes is much the same in all cases, but that of the ventral branches differs greatly in different nerves and must now be followed.

The first spinal nerve is known as the hypoglossal, and corresponds to the twelfth cranial nerve of the mammal. It leaves the neural canal between the first and second vertebræ, curves round the throat, turns forward below the mouth (Fig. 22.40) and proceeds to the tongue. The second spinal nerve is a large strand running straight outwards. It receives branches from the first and third, forming thus the brachial plexus, and proceeds as the brachial nerve to the arm. The third spinal nerve is small, and beyond the brachial plexus resembles the fourth, fifth, and sixth spinal nerves. All these are small and run backwards to supply the muscles and skin of the belly. The seventh, eighth, ninth, and tenth spinal nerves join to form a sciatic plexus, from which arise several nerves to join the hind limb, the principal being the very large sciatic nerve which runs below the dorsal surface of the thigh between the semimembranosus and biceps femoris muscles. The tenth nerve leaves the vertebral canal by a foramen in the side of the urostyle. The roots of the last four pairs of nerves do not issue from the spinal canal at once, but run backwards for some distance from their origin to reach their point of exit. Thus they form inside the vertebral canal a bundle known as the cauda equina.

BRAIN

The brain (Fig. 22.41) may be divided into three regions, known respectively as the hind, mid, and fore brain. The hind brain consists of the medulla oblongata and the cerebellum. The medulla oblongata is the hindermost part of the brain. It is continuous behind with the spinal cord, which, as it is traced into the brain, widens, the central canal enlarging into a cavity in the medulla known as the fourth ventricle of the brain, the ventral side thickening, and the dorsal thinning out into a slight membrane over the fourth ventricle (Fig. 22.41, I). The pia mater above this

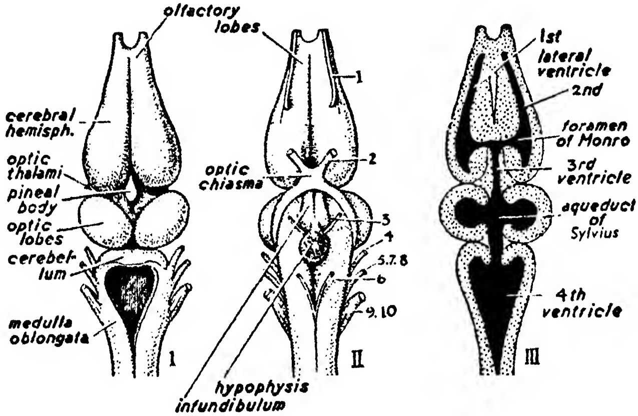


FIG. 22.41.—Brain of a frog.—From Thomson, after Wiedersheim. *I*, Dorsal aspect; *II*, Ventral aspect (the numbers indicate the origins of the nerves); *III*, Horizontal section.

membrane is very vascular and thrown into folds which project into the ventricle, forming thus a structure known as the posterior choroid plexus. The cerebellum is a narrow band across the roof of the front part of the fourth ventricle. In many other animals it is relatively much larger. The midbrain is the region in front of the medulla. It has a thick floor formed by two longitudinal columns known as the crura cerebri, a roof consisting of a pair of rounded swellings known as optic lobes, and internally a narrow passage, the aquæductus Sylvii, continuous behind with the fourth ventricle and above with the cavities in the optic lobes. The fore-brain consists of the thalamencephalon and the cerebral hemispheres. The thalamencephalon lies immediately in front of the midbrain. Its sides are thick and are known as

the thalami ; its roof and floor are thin. The floor is prolonged into a hollow structure known as the infundibulum, which, with a glandular, non-nervous mass called the hypophysis, makes up the pituitary body. The roof is prolonged into a short hollow stalk, which in the tadpole is connected with a structure known as the pineal body. In the adult this has become separated and lies outside the skull. In certain other animals the pineal body is much more highly developed and still connected with its stalk, and its structure shows that it is the remnant of a middle eye, though it is no longer functional. In front of the pineal stalk lies an anterior choroid plexus. The cavity of the thalamencephalon is deep but narrow, and is known as the third ventricle. It is bounded in front by a wall known as the lamina terminalis. Behind this on each side an opening known as the foramen of Monro or foramen interventriculare leads into the cavity or lateral ventricle of one of the cerebral hemispheres. These are oblong-oval bodies narrowing forwards to join a mass which is indistinctly separated into two olfactory lobes. The median walls of the cerebral hemispheres touch in front and behind, but for a considerable distance they are quite separate. Two regions may be distinguished in the wall of each cerebral hemisphere—the ventrolateral region, which is thickened and is known as the corpus striatum, and the rest of the wall, which is the pallium. The brain, like the spinal cord, contains both white and grey matter. Most of the grey matter adjoins the ventricles as that of the spinal cord adjoins the central canal, but the grey layer or cortex which in higher animals overlies the white matter of the pallium (p. 618) is represented by a rudiment.

From the brain proceed several pairs of cranial nerves (Fig. 22.40) ; these follow the same general plan in all vertebrates, but they are best seen and studied in the cartilaginous fishes (pp. 340–341). The chief differences from the dogfish shown by the cranial nerves of the frog are these. V (trigeminal) has all four branches well developed. VI (abducent) supplies, as well as the external rectus, the musculus retractor bulbi of the eye, which surrounds the optic nerve and pulls the eyeball back into its socket ; this muscle is not present in most vertebrates. VII (facial) has neither superficial ophthalmic nor buccal rami, and the lateral line portion of the external mandibular is also missing ; before leaving the skull the facial is closely associated with the trigeminal in a compound pro-otic ganglion, formed by the fusion of the

Gasserian and geniculate ganglia. The pretrematic branch of IX (glossopharyngeal) is absent, and the post-trematic, which contains somatic sensory fibres, supplies the tongue and other structures in the mouth ; there is a connection, known as Jacobson's anastomosis, by visceral sensory fibres from the pharyngeal ramus to the palatine of VII. X (pneumogastric) runs with IX as far as its ganglion ; there is neither pretrematic nor lateral line branch, and the post-trematics are represented by a laryngeal to the muscles of the hyoid and larynx ; the vagus branch supplies the lungs as well as other internal organs. XI (spinal accessory) has a transient existence in the embryo, and XII (hypoglossal) has, by the shortening of the skull, come to lie outside it and appears as the first spinal.

AUTONOMIC SYSTEM

The autonomic or sympathetic system possesses a long nerve-cord on each side of the body below the backbone and alongside the aorta and systemic arch. It is connected by a ramus communicans with each spinal nerve. At the junction of each ramus communicans the sympathetic cord swells into a ganglion. Between the first two ganglia it is double, becoming thus a loop, the annulus of Vieussens or ansa subclavia, through which passes the subclavian artery. In front the longitudinal cord enters the skull with the ninth and tenth nerves, is connected with the tenth, and ends in the Gasserian ganglion. From the sympathetic ganglia small nerves are given off to those of the opposite cord and to the blood vessels and viscera. These nerves break up and rejoin to form networks or plexuses.

SENSE ORGANS

The eyes (Fig. 22.42) have the same general structure as those of mammals, and the image is formed in the same way. The movable lower lid is, like that of the dogfish, a nictitating membrane, or third eyelid. Accommodation for near vision is achieved by protractor lentis muscles, which pull the lens forward. Both rods and cones are present in the retina, and there is a macula where the cones are much more numerous than the rods.

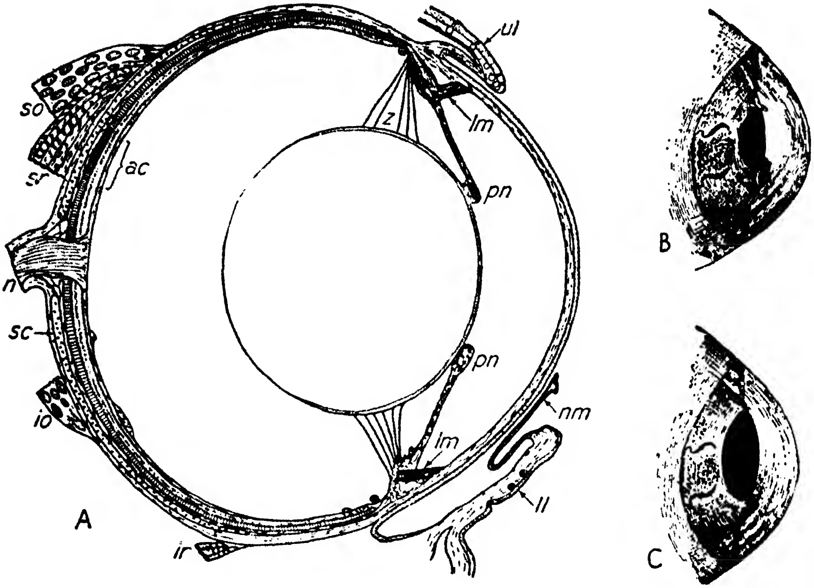


FIG. 22.42.—The amphibian eye and its accommodation.—From Young, *The Life of Vertebrates*, 1950. Clarendon Press, Oxford. After Franz and Beer.

A, Anuran eye in vertical section ; *B*, anterior part of eye of toad (*Bufo*) in relaxation ; *C*, the same in accommodation.

ac, Macular region ; *io*, obliquus inferior ; *ir*, rectus inferior ; *ll*, lower lid ; *lm*, protractor lens muscles ; *n*, optic nerve ; *nm*, nictitating membrane ; *pn*, border of pupil ; *sc*, sclerotic ; *so*, obliquus superior ; *sr*, rectus superior ; *ul*, upper lid ; *z*, suspensory ligaments.

EARS

The essential part of the ear is the membranous labyrinth (Fig. 22.43) which lies in the cavity of the auditory capsule. This cavity contains a fluid known as perilymph, and the membranous labyrinth contains a fluid known as endolymph. The labyrinth consists of the vestibule and the semicircular canals. The vestibule has an upper, larger division, the utriculus, and a lower, smaller sacculus. From the former arise the three semicircular canals, which are arched tubes opening into the utriculus at both ends. They are placed in planes at right angles to one another, one of them being horizontal, another longitudinal-vertical (the posterior vertical), and another transverse-vertical (the anterior vertical). One of the ends of each of them is enlarged to form a small, rounded ampulla. From the sacculus arises an off-shoot known as the lagena which has three small dilatations ; this represents the

cochlea of higher animals. On the median side of the sacculus there starts a tube, the ductus endolymphaticus, which enters the cranial cavity and there expands into a thin-walled sac. Between the auditory capsules and the membrane of the ear-drum or tympanic membrane on the side of the head lies the cavity of the ear-drum or tympanic cavity, which, as we have seen, is crossed by the columella from the fenestra ovalis to the tympanic membrane and communicates with the pharynx by

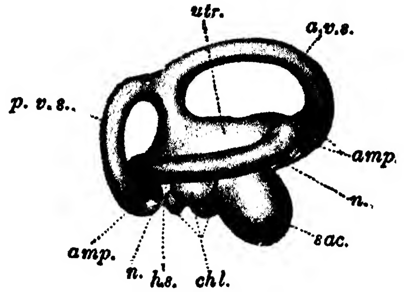


FIG. 22.43.—The labyrinth of the right ear of the frog, seen from the outer side.—Partly after Marshall.

a.v.s., Anterior vertical semicircular canal; *amp.*, ampullæ; *chl.*, small dilatations of the sacculus which represent the cochlea of higher animals; *h.s.*, horizontal semicircular canal; *n.*, branches of the auditory nerve to supply the ampullæ; *p.v.s.*, posterior vertical semicircular canal; *sac.*, sacculus; *utr.*, utriculus.

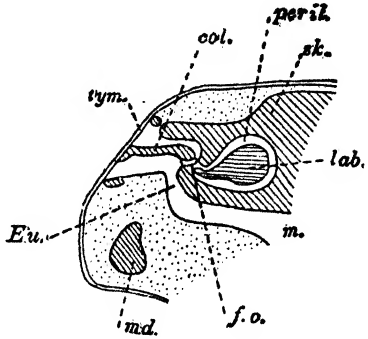


FIG. 22.44.—A diagram of the ear of the frog.

col., Columella; *f.o.*, fenestra ovalis; *Eu.*, Eustachian tube; *lab.*, part of the membranous labyrinth, containing endolymph; *m.*, mouth; *md.*, mandible; *peril.*, perilymph; *sk.*, skull; *tym.*, tympanic membrane.

the Eustachian tube. This region is called the middle ear, the labyrinth being the inner ear. There is no outer ear in the frog.

FUNCTIONS OF THE EARS

The semicircular canals and utriculus are not organs of hearing, but enable the animal to keep its balance by judging the position of its head. Placed as they are in three planes of space, the fluid in them is set in movement by any change in position, and the differences in pressure on their walls which are thus brought about start impulses which the auditory nerve conveys to the brain. The true organ of hearing is the sacculus. The vibrations which constitute sound set the tympanic membrane in motion, and its movements are transferred by the columella to the membrane of the fenestra ovalis and thence through the perilymph

and the wall of the membranous labyrinth to the endolymph, where they stimulate the endings of the auditory nerve in the dilatations of the saccule. Frogs appear to be able to respond to sounds up to a frequency of about 500 cycles a second.

OLFACTORY ORGANS

The organs of smell are a pair of irregular chambers, enclosed by the nasal capsules, separated by the nasal septum, and communicating with the exterior by the nostrils and with the mouth by the internal nares. The lining of each is connected with the olfactory nerve of its side. Air is drawn through the chambers in the process of breathing, and the odorous particles it contains affect certain cells of the lining which are connected with fibres of the nerve. Anurans, however (p.549), seem to be relatively insensible to smell.

23

THE PIGEON

THE pigeons of our dovecots are descendants of the wild rock dove (*Columba livia*) which is no longer found in the wild state in England and Wales, although it still breeds on the north-west coast of Scotland and the adjacent islands. Although many

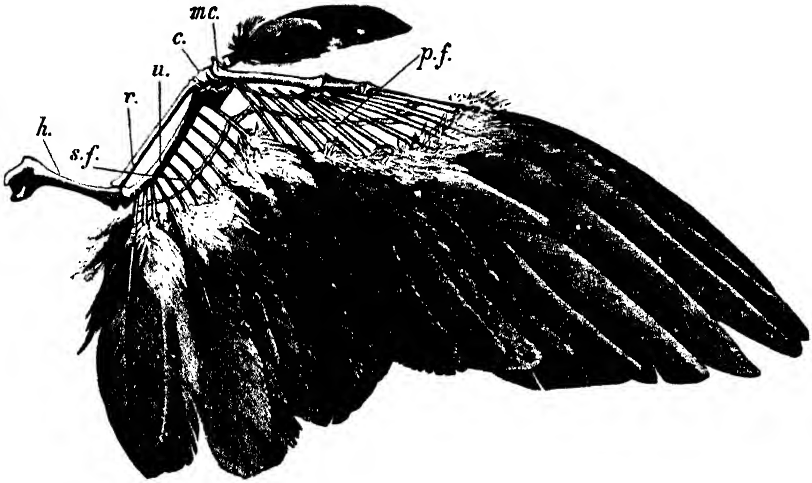


FIG. 23.1.—The wing of a dove. From Thomson.

c., Carpals; *h.*, humerus; *mc.*, carpo-metacarpus; *p.f.*, primary feathers; *r.*, radius *s.f.*, secondary feathers; *u.*, ulna.

of the domestic forms, such as fantails and pouters, have diverged greatly from the ancestral stock, the feral birds, which are those usually dissected, closely resemble the wild type.

EXTERNAL FEATURES

The pigeon has a boat-shaped body which offers little resistance to the air, and a coat of feathers, which affords a light and warm covering. A distinct head, neck, and trunk are present, but the tail is a mere stump which bears a fan of long feathers. The fore-limbs are wings and the legs have their skeleton modified to support the whole weight of the body. The feet are naked and covered with scales, which are horny and epidermal like those of a reptile, not like those of a fish. There are four toes, which

have a wide tread, the first being directed backwards and the other three forwards; the fifth is wanting. The front or facial portion of the head is drawn out into a beak covered with horny skin. At its base above is a swollen, featherless patch of skin, the cere. The nostrils lie below the cere, the eyes behind it at the sides of the head, and the ear openings below and behind the

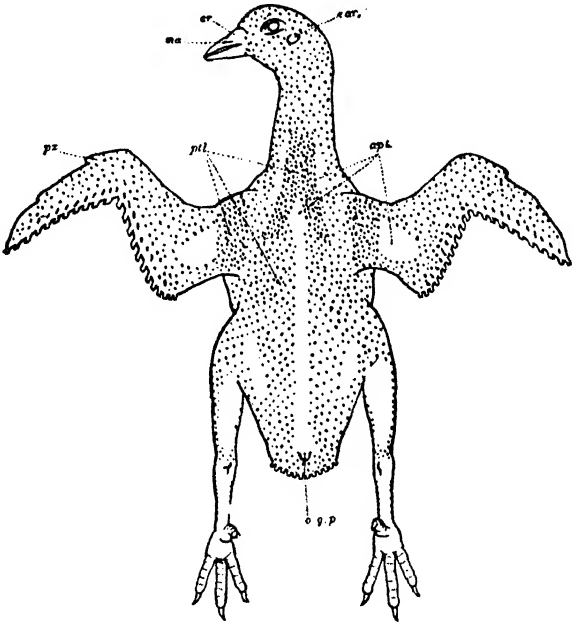


FIG. 23.2.—A plucked pigeon, seen in dorsal view.

apt. Apteria; *cr.*, cere; *ear*; *na.*, nostril; *o.g.p.*, papilla on which the oil gland opens; *ptl.*, pterylæ; *px.*, thumb.

eyes, covered by feathers. There are three movable eyelids and the drum of the ear is at the bottom of a tube, but there is no ear flap. There is a single cloacal opening, as a transverse slit below the tail, and above the tail is a knob on which opens the oil gland, the secretion of which is used in preening the feathers.

FEATHERS

The most conspicuous feathers, and the most important for the bird, are those of the wing. They are grouped, and partly

named, according to the bones which give them support, as follows :

BONE	FEATHERS		
Humerus	Humerals		
Ulna	Secondaries or cubitals		Remiges (singular remex)
Metacarpal II	Metacarpal quills	Primaries	Remiges (singular remex)
Digit II	Digitals	Primaries	Remiges (singular remex)
Digit I	Ala spuria or bastard wing		

The remiges, which are the largest feathers, are firmly based in the bone ; they are covered, above and below, by several series

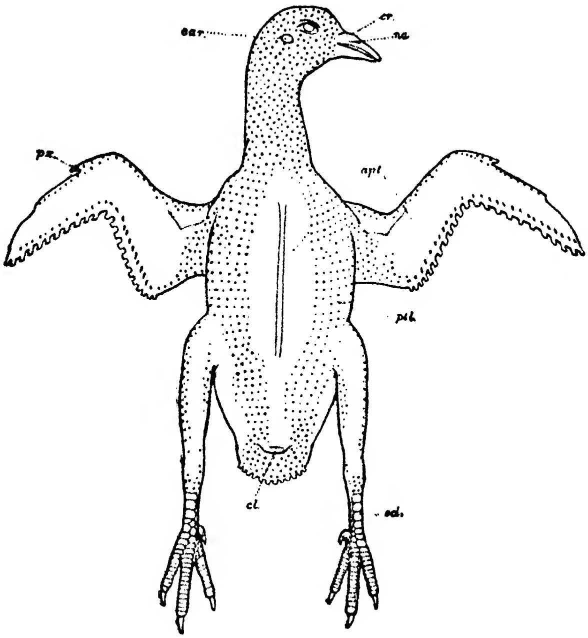


FIG. 23.3.—A plucked pigeon, seen in ventral view.

apl., Apteria ; *cl.*, cloacal opening ; *cr.*, cere ; *ear* ; *na.*, nostril ; *ptl.*, pteryla ; *px.*, thumb ; *scl.*, scales on foot.

of smaller feathers called coverts, or tectrices, to which series the humerals belong. The coverts are based in the skin, of which two loose folds, the propatagium and postpatagium, connect the shoulder with the anterior and posterior borders of the fore-arm respectively. The pigeon has eleven primaries, of which the

first, as in many other birds, is small and not easily visible. The bastard wing is a small tuft of feathers at the wrist. The tail bears twelve large feathers called rectrices and many coverts. The rest of the body is covered with numerous smaller feathers ; these are not uniformly distributed, but grow in tracts or pterylæ, separated by bare patches or apteria (Figs. 23.2, 23.3).

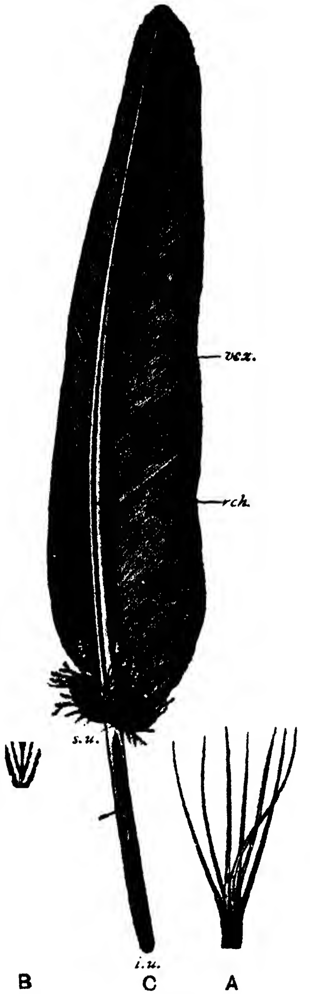


FIG. 23.4.—Feathers of a pigeon.

A, Down feather ; *B*, filoplume, *C*, quill feather.

a.s., Aftershaft ; *i.u.*, inferior umbilicus ; *qu.*, quill or calamus ; *rch.*, rachis or shaft ; *s.u.*, superior umbilicus ; *vex.*, vexillum or vane.

The structure of a feather is best seen in a quill or one of the larger coverts (Fig. 23.4). The stem or scapus is divided into a lower, hollow part, the calamus or quill, and an upper, solid part, the rachis. The quill is embedded in a pit of the skin and has at its lower end an opening, the inferior umbilicus, through which a vascular papilla projects into the growing feather. At the junction of the quill and rachis is a minute opening known as the superior umbilicus. Close to this arises a small tuft known as the aftershaft. The rachis is the axis of the flattened part of the feather known as the vexillum or vane. This is composed of a series of elastic plates set along the sides of the rachis with their flat sides perpendicular to the plane of the vane. The plates are known as barbs (Fig. 23.5), and they are held together by barbules, which are smaller processes that fringe the barbs. The barbules of one side of a barb (distal barbules) bear little hooks or barbicels which catch upon the barbules of the adjoining barb. Thus the whole vane is held together and forms a single surface for striking the air.

Each feather develops as an ectodermal papilla with a mesodermal plug (Fig. 23.6) ; the papilla grows at its base, and so elongates to form a cylinder ; this splits and unfolds to form the rachis and vane ; a double split at the base gives the after-shaft, which in some birds such as the emu is greatly developed

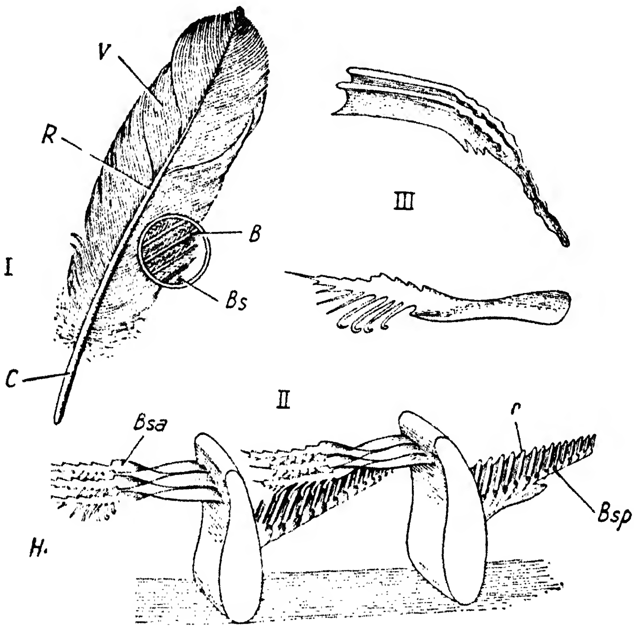


FIG. 23.5. The structure of a feather.—From Young, *The Life of Vertebrates*, 1950. Clarendon Press, Oxford.—After Pycraft.

I, Whole feather with a small portion as seen under a lens : *II*, block section of barbs in the plane of the barbules ; *III*, one anterior and two posterior barbules ; *B*, barb ; *Bs*, barbule ; *Bsa*, anterior barbule ; *Bsp*, posterior barbule ; *C*, calamus ; *H*, hamulus ; *R*, rachis ; *r*, ridge on posterior barbule which interlocks with hamulus ; *V*, vane.

so that the feather is double. Variations on the general plan of development give different types of feathers ; the contour feathers of the body have poorly-developed barbules, so that the barbs are easily separated ; scattered over the body are filoplumes, in which a fine rachis has a small tuft of barbs at the apex, and down feathers, which consist of a tuft of barbs with no rachis. Feathers are shed or moulted and replaced at intervals ; most birds have a single annual moult, in the autumn, but in some there are two.

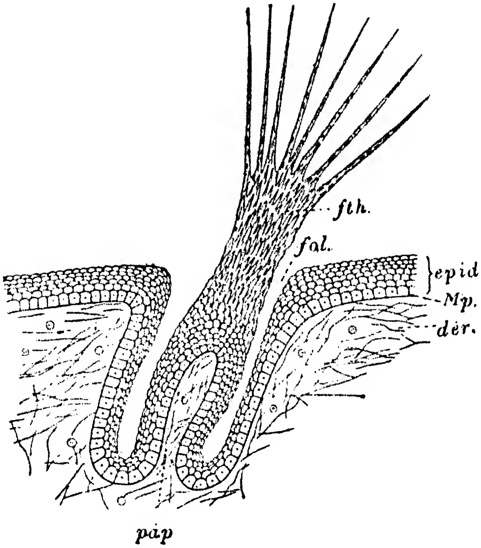


FIG. 23.6.—A diagram of a developing feather, highly magnified.—From Shipley and MacBride.

der., Dermis; *epid.*, epidermis; *fol.*, follicle; *fth.*, feather; *Mp.*, Malpighian layer of epidermis; *pap.*, papilla by the growth of whose epidermis the feather is formed.

FLIGHT

Bird flight is complex, and no complete dynamic account of it has ever been given. It may be assumed on the principles of Newtonian mechanics that in flapping flight the wing must exert a force on the air which has a downward component to resist the bird's weight, and a backward component to overcome air resistance; both must be large enough at times to provide acceleration. Photographs of birds in flight leave no doubt that wings go into most peculiar positions, and it may be assumed that they do so in order to produce the necessary force. A recent cinematograph film of the pigeon in slow flight (as at take-off) (Fig. 23.7) suggests that the downstroke produces nearly all lift (i.e. downward force) and the upstroke mainly thrust (i.e. backward force) with some lift in its earlier phases; in normal flight both thrust and lift come almost entirely from the downstroke and the wing moves in a much simpler up-and-down fashion. It is obvious that the relative proportions of lift and thrust can be altered by alterations in the attitudes of the wings. In gliding, which the pigeon uses only when about to land and in sexual

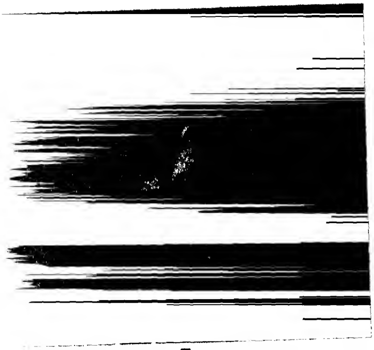
display, the wings are held motionless, and the air pressure produced by the horizontal velocity previously obtained by flapping, produces, because of the shape of the wing, a lift which reduces the rate of fall. In soaring flight, which the pigeon does not use, birds are carried upwards on outspread wings in vertical air currents. Many of the special features of aeronautics can be seen in bird wings and flight. Thus the wings are cambered from fore to aft to increase lift, and for the same purpose a slotted wing is often produced by the separation of the primaries in flight (Fig. 23.7, 2). In many birds this effect is increased by the emargination of the feathers ; that is, the front part of the vane is narrowed for part of its length. The tail feathers assist in braking and steering.

SKELETON

The pigeon has a chest or thorax, walled by ribs and a broad breastbone, but lacks the midriff or diaphragm of mammals. The bones are very light and spongy in texture, and most of them, except those of the tail, forearm, hand, and hind-limb, contain air spaces. A tendency to the fusion of bones is seen in various regions, and the proportion of cartilage is very small. The centra of the free vertebræ (Fig. 23.8) are distinguished from those of all other vertebrates in being heterocœlous, that is, their surface is like that of a saddle, or col of a hill, convex in one direction and concave in the other ; the front surface has the concavity running from side to side. The backbone is divided into five regions : (1) The neck contains thirteen to fifteen cervical vertebræ, the commonest number being fourteen. The atlas is procœlous. The third to the eleventh or twelfth cervical vertebræ bear short ribs fused to the centra and transverse processes. The ribs of the last two are free, but do not reach the breastbone. (2) Behind these come five thoracic vertebræ, whose ribs reach the breastbone. Of these the first three are fused together, the fourth is free, and the fifth is fused with those behind it. (3) The next half-dozen vertebræ are called lumbar and are fused in front with the last thoracic and behind with (4) the two sacral and (5) the first five caudal. Thus there is a long group of fused vertebræ, known as the sacrum, to which the pelvic girdle is attached. Then follow six free caudal vertebræ and the ploughshare bone or pygostyle, which consists of four fused vertebræ and supports the tail. Each rib has a head or capitulum which

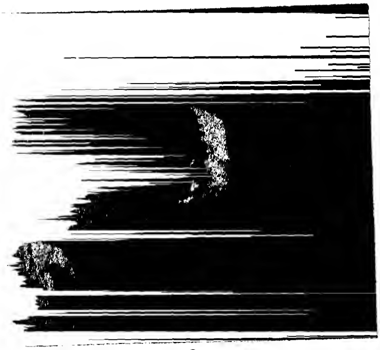
FIG. 23.7.—Photographs of a tame pigeon in slow flight. Ninety-one pictures per second.—From Brown, *J. exp. Biol.*, 1948, 25, 322.

1. Early part of downbeat. Alula opened. Forward force on primaries 1 and 2.
2. Wing horizontal.
3. Beginning of forward swing.
4. End of downward movement, forward movement continuing.
5. Beginning of upstroke.
6. Upstroke. Primaries uncurved—no external work being done.

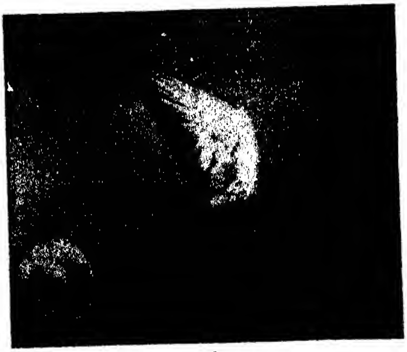


7

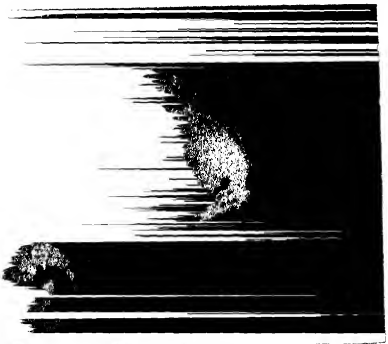
8



9



10

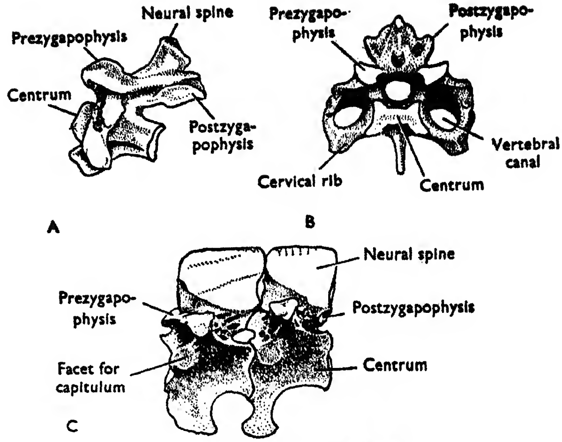


11

12

7. Beginning of flick of wings. Primaries beginning to be bent by upward pressure of air.
8. Full development of flick.
9. Extension of wing.
10. Completion of upstroke.
11. Wing still extending, but passive.
12. Beginning of downstroke. Alula starting to open.

FIG. 23.8.—Vertebræ of a turkey. *A*, cervical, from the left side ; *B*, cervical, from in front ; *C*, two thoracic vertebræ, from the left side. × 1.



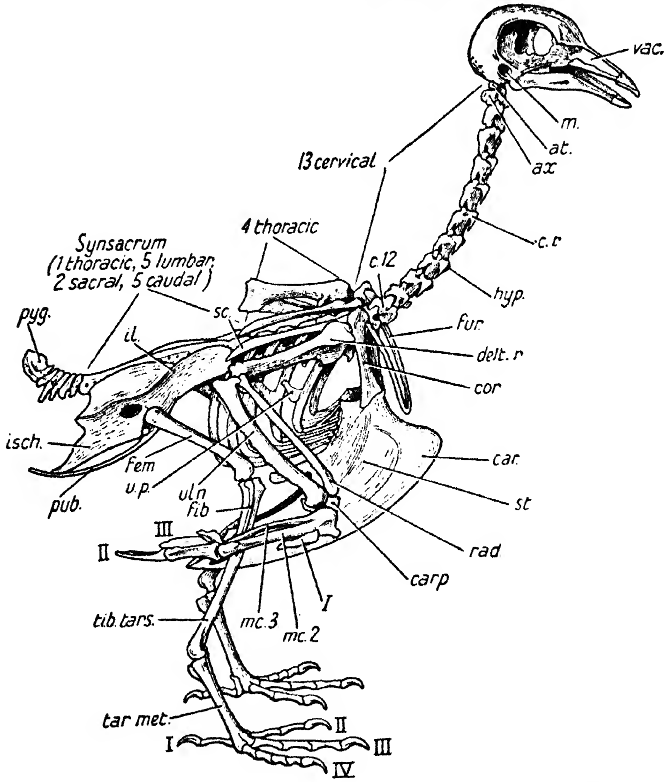


FIG. 23.9.—Skeleton of a pigeon.—From Young, *The Life of Vertebrates*, 1950. Clarendon Press, Oxford.

at., Atlas ; *ax.*, axis ; *c.* 12, twelfth cervical vertebra ; *car.*, keel ; *carp.*, carpus ; *cor.*, coracoid ; *c.r.*, cervical rib ; *delt.r.*, deltoid ridge ; *fem.*, femur ; *fib.*, fibula ; *fur.*, furcula ; *hyp.*, hypapophysis ; *il.*, ilium ; *isch.*, ischium ; *m.*, auditory meatus ; *mc.*2, second, and *mc.*3, third metacarpal ; *pub.*, pubis ; *pyg.* pygostyle ; *rad.*, radius ; *sc.*, scapula ; *st.*, body of sternum ; *tar.met.*, tarsometatarsus ; *tib.tars.*, tibiotarsus ; *uln.*, ulna ; *u.p.*, uncinate process ; *vac.*, vacuity in skull ; I-IV digits.

articulates with the centrum of its vertebra and a tubercle which articulates with the transverse process. Those which join the sternum are bent forwards at an angle to do so, the part above the angle being known as the vertebral rib, that below as the sternal rib. Both parts are bony in the pigeon, whereas in the rabbit the sternal ribs are cartilaginous. On the hinder side of each of the free ribs, except those of the last pair, is an uncinate process.

THE SKULL

The skull (Figs. 23.10, 23.11) has very large orbits, which are situated almost entirely in front of the cranium, so that the eyes are separated not by the whole width of the brain, but merely

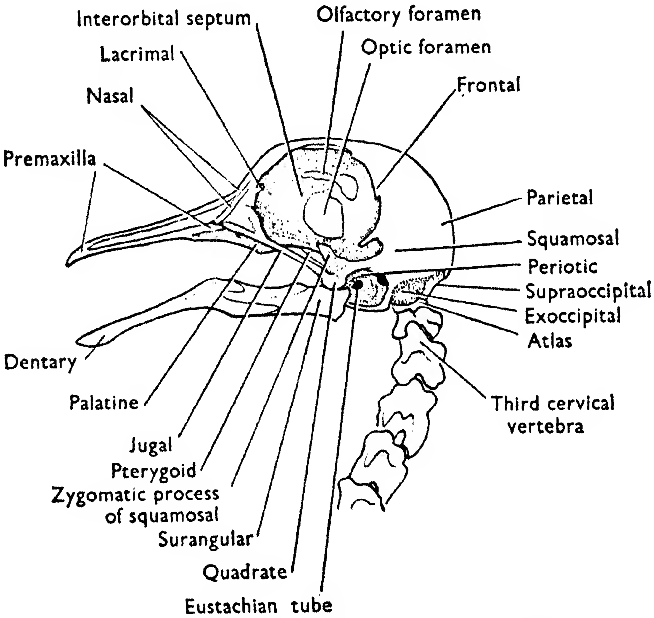


FIG. 23.10.—Pigeon. The skull and the upper cervical vertebræ, from the left side. × 1.

by an interorbital septum. In the adult, separate bones can hardly be distinguished in the skull, and the following account is based on what can be seen in the embryo and young bird, particularly in the domestic fowl.

The foramen magnum is surrounded by basioccipital, supra-occipital, and two exoccipitals, and there is a single condyle

formed mainly by the basioccipital. In front of the basioccipital is the basisphenoid, and above this on each side the wall of the cranium is partially formed of an alisphenoid. The front of the cranium, and the interorbital septum, consist of a single bone representing mesethmoid, pre-sphenoid, and orbitosphenoids. The remainder of the cranium is formed of membrane bones; parietals and frontals in the roof and small lacrimals in front of and above the orbits. Below the basiphenoid is a pair of bones sometimes called basitemporals, which represent the posterior part of the parasphenoid of the frog, and a piece of membrane bone representing the front end of this is fused on to the inter-orbital septum to form the rost-rum. The basitemporals and the rostrum all become fused to the basisphenoid. The auditory capsule consists of a single peri-otic below the parietal, and in front of the capsule a squamosal completes the covering of the

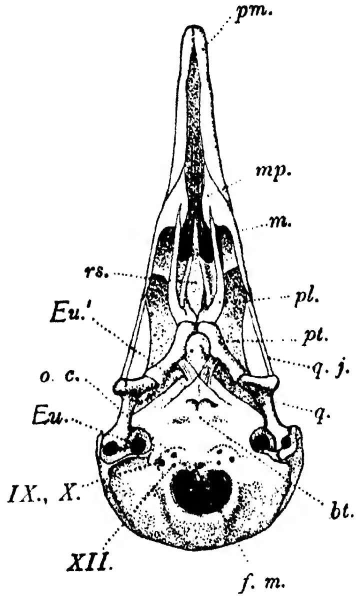


FIG. 23.11.—The skull of a pigeon, from below.

bt., Basitemporal; *Eu.*, hinder opening of passage for Eustachian tube; *Eu'.*, anterior opening of the same; *f.m.*, foramen magnum; *m.*, maxilla; *mp.*, maxillopalatine process; *o.c.*, occipital condyle; *pl.*, palatine; *pm.*, pre-maxilla; *pt.*, pterygoid *q.*, quadrate; *q.j.*, quadratojugal; *rs.*, rostrum; *IX.*, *X.*, *XII.*, foramina for cranial nerves.

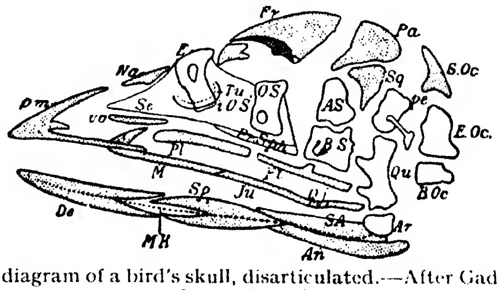


FIG. 23.12.—A diagram of a bird's skull, disarticulated.—After Gadow. Membrane bones shaded.

B.Oc, Basioccipital; *E.Oc.*, exoccipital; *S.Oc.*, supraoccipital; *Pa.*, parietal; *Fr.*, frontal; *Na.*, nasal; *pm.*, premaxilla; *M.*, maxilla; *Ju.*, jugal; *Qj.*, quadratojugal; *Qu.*, quadrate; *Pl.*, palatine; *Pt.*, pterygoid; *pe.*, periotic; *Sq.*, squamosal; *AS.*, alisphenoid, *B.S.*, basisphenoid; *O.S.*, orbitosphenoid; *Pr.Sph.*, presphenoid; *vo.*, vomer; *iOS.*, interorbital septum; *E.*, ethmoid; *Se.*, nasal septum; *De.*, dentary; *Sp.*, splenial; *An.*, angular; *S.A.*, supra-angular; *Ar.*, articular; *MK.*, Meckel's cartilage; *Tu.*, cartilaginous turbinal.

brain. The nasal capsules are fused with the interorbital septum. Above them is a pair of nasals, deeply notched in front for the nostrils. The vomers are vestigial in the pigeon, but in the fowl are represented by a slender median rod in front of the rostrum. The upper jaw is completely ossified ; the quadrate is a conspicuous three-branched bone articulated with the squamosal, the pterygoid, the quadratojugal, and the lower jaw, and from it the pterygoid runs forwards and slightly inwards to meet the rostrum. From the pterygoid the palatine continues forwards to the nasal capsule. The quadratojugal is a slender splint running forward to the maxilla, which is also small and lies inside the premaxilla ; on its inner surface it has a plate-like projection, the maxillopalatine process. The premaxilla completes the upper jaw ; it has two backwardly directed processes which, with the nasal, enclose the external nostril, and the outer of these runs back outside the front part of the maxilla. In front the premaxilla bears the beak. The connections of the palatines with the pterygoids and of the pterygoids with the quadrates, are articulations, not sutures, so that there is some movement of the upper jaw on the cranium ; in parrots the nasals are also articulated to the frontals, so that when the mouth opens the whole upper jaw is raised.

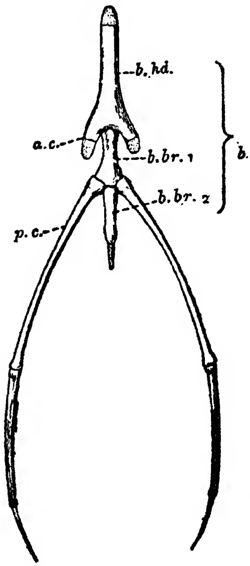


FIG. 23.13.—The hyoid apparatus of a pigeon.

a.c., Anterior cornu ; *b.*, body of the hyoid ; *b.br.1*, *b.br.2*, basibranchials ; *b.hd.*, basihyoid ; *p.c.*, posterior cornu.

In the slender lower jaw, articular, angular, surangular, dentary, splenial, and in some birds prearticular, elements can be made out. There is a columella auris and a slender, mainly bony, forked hyoid apparatus supporting the tongue (Fig. 23.13).

LIMBS

The shoulder girdle contains narrow, sabre-like scapulæ, stout coracoids which slope down to join the sternum, and slender clavicles which are joined to each other by a disc-shaped

interclavicle, the three bones together making the 'merry thought' or furcula. Where scapula, coracoid, and clavicle join, a small opening, the foramen triosseum, is left between them. The sternum is a broad plate, bearing below a conspicuous median keel or carina for the attachment of the great wing muscles, behind two xiphoid processes, at the sides facets for the ribs, and in front surfaces

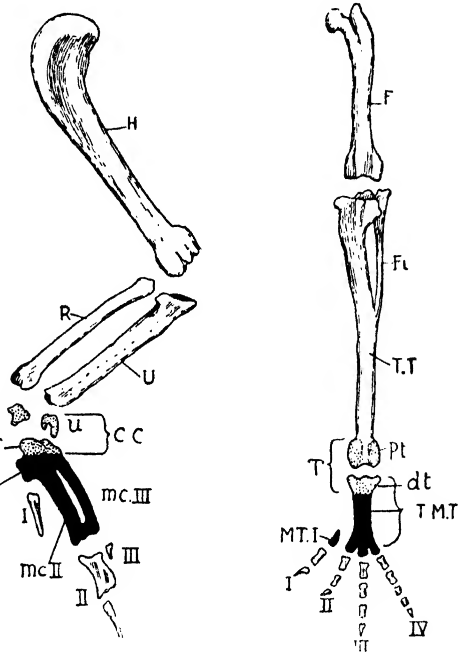


FIG. 23.14.—The fore-limb and hind-limb of a bird compared. From Thomson.

H., Humerus; *R.*, radius; *U.*, ulna; *r.*, radiale; *u.*, ulnare; *C.*, distal carpals united to carpometacarpus *CC.*, the whole carpal region; *mc.I.*, metacarpal of the thumb; *I.*, phalanx of the thumb, *mc.II.*, second metacarpus; *II.*, second digit; *mc.III.*, third metacarpus; *III.*, third digit; *F.*, femur; *T.T.*, tibiotarsus; *Fi.*, fibula; *Pt.*, proximal tarsals united to lower end of tibia; *dt.*, distal tarsals united to upper end of metatarsus, forming a tarsometatarsus (*T.M.T.*); *T.*, entire tarsal region; *MT.I.*, first metatarsal, free; *I.–IV.*, toes.

for the articulation of the coracoid bones. In the wing skeleton (Fig. 23.14) there is a short, stout humerus, a parallel radius and ulna, rather widely separated except at their ends, where they touch, and two free carpal bones, which are the radiale and ulnare. The bones of the distal row have fused with three metacarpals to form a single carpometacarpus. There are only three digits, the phalangeal formula being 12100.

In the pelvic girdle there is a long ilium, reaching a good way behind as well as in front of the acetabulum, and connected

with the sacrum along nearly the whole of its inner side to form a single structure, the synsacrum. This long bone enables the trunk to be supported in a more or less horizontal position by the single pair of legs. The acetabulum is placed near the middle of the ilium. The ischium is a flat, backwardly directed bone. Its hinder part is fused with the ilium, but just behind the acetabulum an oval opening—the iliosciatic foramen—lies between the two. The pubis is slender and also directed backwards. In many birds it has a small prepubic or pectineal process in front. The obturator foramen is slit-like. There is no symphysis or ventral junction of the girdles. The hind-limb has a short, stout femur, and below this is a long tibiotarsus, made up of the tibia and the proximal tarsals. The slender fibula is free above but fused with the tibiotarsus below. The distal tarsals are fused with metatarsals 2 to 4 to form a single tarsometatarsus, which has a characteristic trifid end. The first metatarsal is free, and there are four digits, with phalangeal formula 23450.

MUSCULAR ARRANGEMENTS

The most conspicuous part of the muscular system is the great pectoral muscles. The pectoralis major, arising from the sternum and clavicle, is inserted on the under side of the humerus, which it pulls downwards. The smaller pectoralis minor arises from the sternum above the major and passes through the foramen triosseum and over the shoulder to its insertion on the upper side of the humerus, which it raises. The perching mechanism is also interesting. The flexor tendons which curve the toes round a branch are so arranged that they are tightened by the bending of the metatarsus on the tibia in perching, so that the bird does not fall even when it is asleep.

ALIMENTARY SYSTEM

The mouth has no teeth or true palate (false roof, p. 435), but there are large posterior nares partly hidden by soft palatal folds, a single opening for the Eustachian tubes, and a sharp-pointed tongue. The glottis is not protected by an epiglottis as in the rabbit. The gullet widens into a thin-walled crop (Fig. 23.15), in which the food is stored. From the crop the gullet continues

to the stomach, which has two parts, first the fore-stomach or proventriculus, which has glands which secrete the gastric juice, and then the gizzard or muscular stomach, a lens-shaped

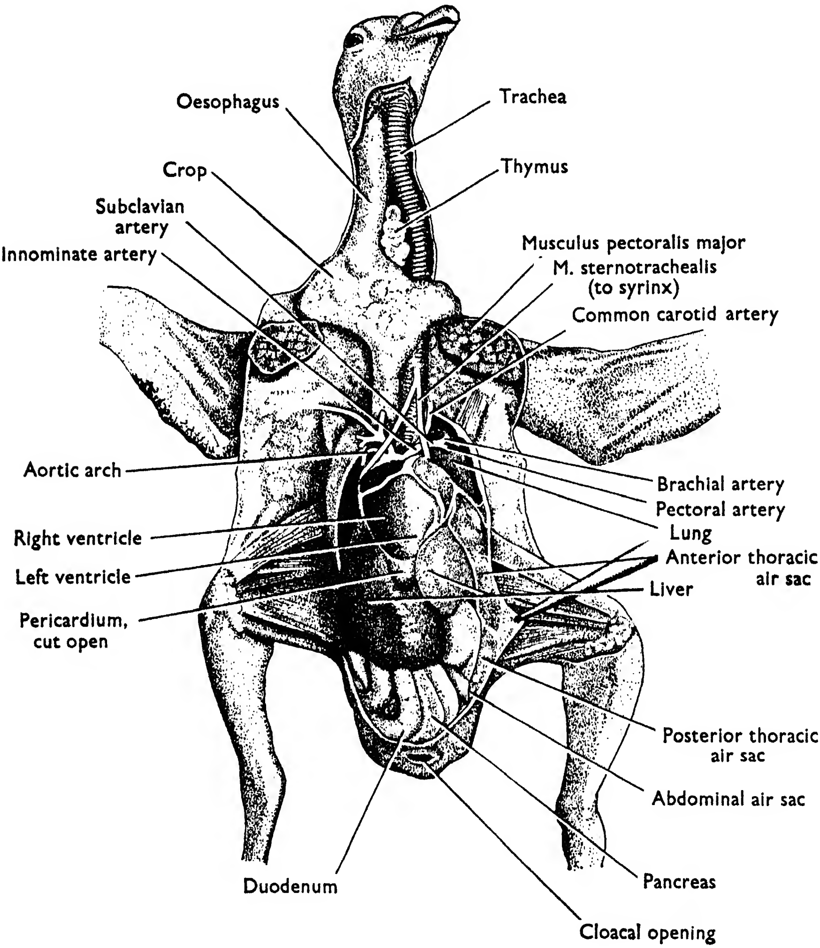


FIG. 23.15.—Pigeon. Dissection from the ventral surface; the body wall is laid back, and the sternum and most of the pectoral muscles have been removed. × 0·5.

chamber with very thick muscular walls and a horny lining, where the food is ground up by the aid of small stones which have been swallowed. It lies below the proventriculus, which opens on its dorsal border, rather to the left side: on the right side

near the same spot is the opening of the duodenum. This is a V-shaped loop, between whose limbs lies the pancreas. The ducts of this gland are three, and all open into the distal limb of the duodenum, two about the middle of its length, and one, which is longer than the others, near the end. There are two bile ducts, which run from the large, bilobed liver and join the duodenum, the wide left duct opening into the proximal limb and the narrower right duct into the distal limb near the first two pancreatic ducts. There is no gall-bladder in the common pigeon. The ileum is a much-coiled tube about two and a half feet in length. The rectum is about an inch and a half long. Its beginning is marked by a pair of small rectal cæca; behind it opens by an anus into the cloaca (Fig. 23.16). This has three regions separated by shelves of the wall. The first and largest is the coprodæum into which the rectum opens, the small middle division is the urodæum into which the urinary and generative ducts open, the third, larger, is the proctodæum; upon its dorsal surface there opens in the young a glandular sac, the bursa Fabricii, of unknown function.

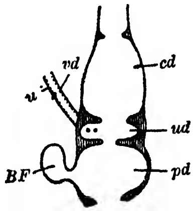


FIG. 23.16.—A diagrammatic section of the cloaca of a male bird.—After Gadow.

cd., Upper region of cloaca into which rectum opens; *ud.*, median region into which ureter (*u.*) and vas deferens (*vd.*) open from each side; *pd.*, posterior region into which bursa Fabricii (*B.F.*) opens.

The digestive processes show some peculiarities. There is some digestion in the crop, mainly by autolysis and bacterial attack, and it has been shown that in the fowl the grinding in the gizzard is necessary for the digestion of coarse corn; finely ground corn could be dealt with by birds from whom the gizzard had been removed. The gizzard contents in the pigeon are highly acid (pH 2·0) but in the proventriculus the acidity is less (pH 4·8), and there seems to be a poor supply of pepsin. The intestinal contents at pH 5·3–5·5 are more acid than in mammals. Most species of bird do not have a crop, and many are without a gizzard.

The spleen is a small red body, attached to the right side of the proventriculus.

RESPIRATORY ORGANS

The glottis, behind the root of the tongue, opens into the voiceless larynx, from which the long trachea (Fig. 23.15),

strengthened with bony rings, leads back along the neck, lying at first below the gullet and then at its left side. At the base of the neck it divides into the two bronchi ; the hinder end of the

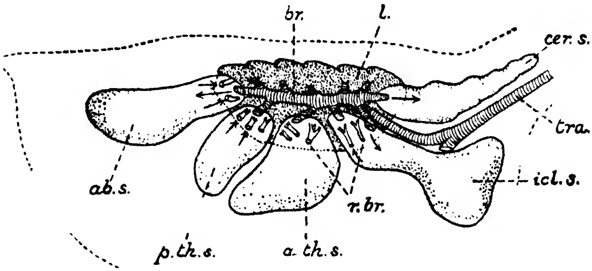


FIG. 23.17.—A diagram of a lung and its air sacs in the pigeon.

ab.s., Abdominal sac ; *a.th.s.*, anterior thoracic sac ; *br.*, bronchus ; *cer.s.*, cervical sac ; *icl.s.*, interclavicular sac ; *l.*, lung ; *p.th.s.*, posterior thoracic sac ; *r.br.*, recurrent bronchi ; *tra.*, trachea. The arrows show the direction of the air currents.

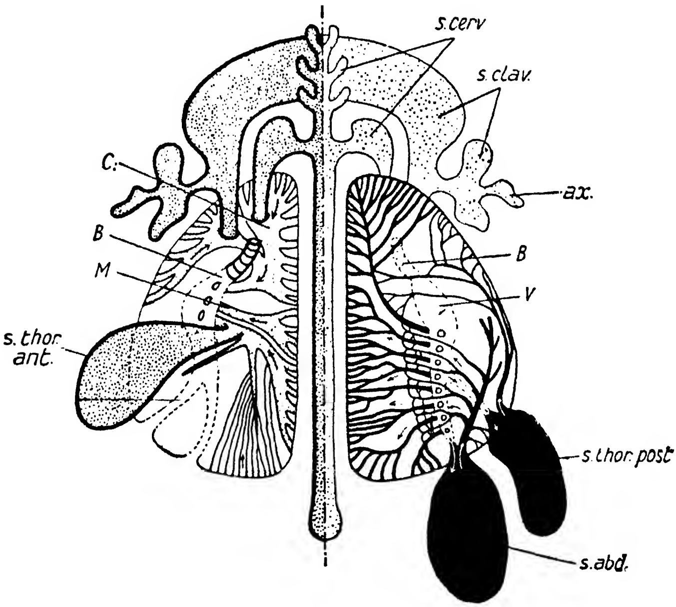


FIG. 23.18.—Diagram of the lungs and air sacs of the pigeon. On the left : the ventral surface of the lungs, the expiratory bronchi, and air sacs. On the right : the inspiratory bronchi and air sacs in black.—From Young, *The Life of Vertebrates*, 1950. Clarendon Press, Oxford. After Brandes and Ihle.

B., Main bronchus ; *C.*, cervical ventro-bronchus ; *M.*, mesobronchus ; *V.*, vestibule ; *s.abd.*, abdominal air sac ; *s.cerv.*, cervical air sac ; *s.clav.*, clavicular air sac with diverticulum (*ax.*) in axilla ; *s.thor.ant.*, anterior and *s.thor.post.* posterior, thoracic air sac.

trachea is dilated and forms, with the beginnings of the bronchi, the syrinx or organ of voice. Sound is produced by the vibration of the membrana semilunaris, a delicate vertical fold of mucous membrane, extending forwards from the angle between the bronchi. The main trunks of the bronchi run right through the lungs, which lie against the dorsal walls of the thorax covered with peritoneum below only, into a series of large air sacs. These are membranous cavities, seen when the sternum is removed in dissection (Fig. 23.17). The median interclavicular sac, and some of the others, send extensions into the bones. Inspiration is a passive fall of the sternum, which draws air into the sacs ; in expiration the sternum is raised, and the air is forcibly expelled through recurrent bronchi into a network of air capillaries in the lungs, and so by the main trunks of the bronchi into the exterior. Expiration is thus the active phase, and it is during this that the chief gas exchange takes place (Fig. 23.18).

BLOOD VESSELS

The body temperature is 42° C., which is higher than that of mammals. This fact is no doubt connected with the active life of the bird and the rapid metabolism which it necessitates. We have already seen how the respiratory organs provide the ample supply of oxygen which such metabolism demands. The red corpuscles are oval and nucleated. The heart has four chambers, two auricles and two ventricles, there being no sinus venosus or conus arteriosus. The deoxygenated blood returned by the venæ cavæ to the right auricle passes into the right ventricle through an opening guarded by a muscular valve without chordæ tendineæ. It is then driven by the pulmonary artery to the lungs, whence it returns by the pulmonary veins to the left auricle, passing thence through two membranous valves with chordæ tendineæ to the left ventricle, by which it is driven into the single aortic arch. The openings of the aorta and pulmonary artery are guarded each by three semilunar valves. The aortic arch bends over to the right side, giving off at its apex right and left innominate arteries, from each of which arise a carotid and a subclavian. The latter is not a true subclavian, being an expansion of a segmental artery, and is exceedingly short, breaking up immediately into brachial and pectoral branches. The further course of the arteries is shown in Fig. 23.19. The venous system is

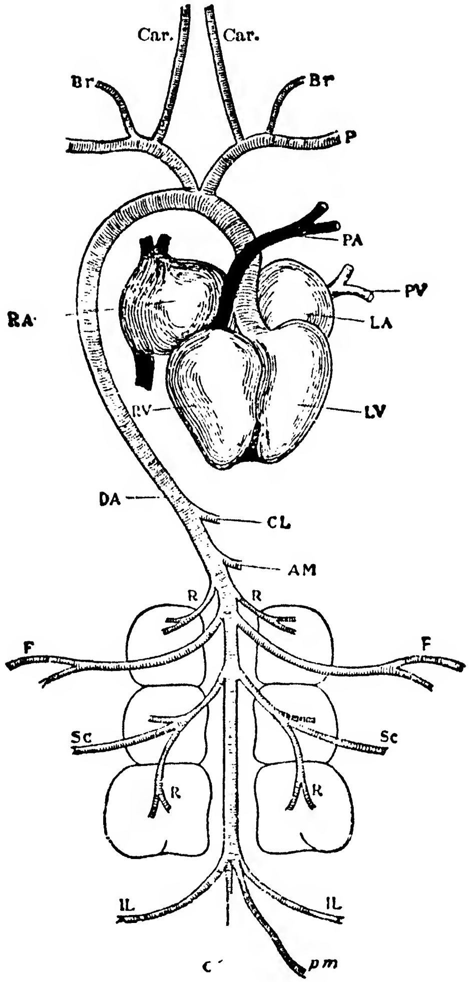


FIG. 23.19.—The principal arteries of a pigeon.—From Thomson.

A.M., Anterior mesenteric; *Br.*, brachial; *C.*, caudal; *Car.*, carotid; *CL.*, cœliac; *D.A.*, dorsal aorta; *F.*, femoral; *IL.*, iliac; *L.A.*, left auricle; *L.V.*, left ventricle; *P.*, pectoral; *P.A.*, pulmonary artery; *P.V.*, pulmonary vein; *p.m.*, posterior mesenteric; *R.*, renals; *R.A.*, right auricle; *R.V.*, right ventricle; *Sc.*, sciatic.

shown in Fig. 23.20. There are three venæ cavæ, as in the frog. Each superior vena cava is formed by the union of a jugular, a brachial, and a pectoral vein. The jugulars anastomose under the base of the skull. The inferior vena cava arises by the junction

of two iliac veins in front of the kidney. Each iliac vein is formed by the union of a femoral, a renal, and a big hypogastric which passes upwards through the kidney. Behind the kidneys the

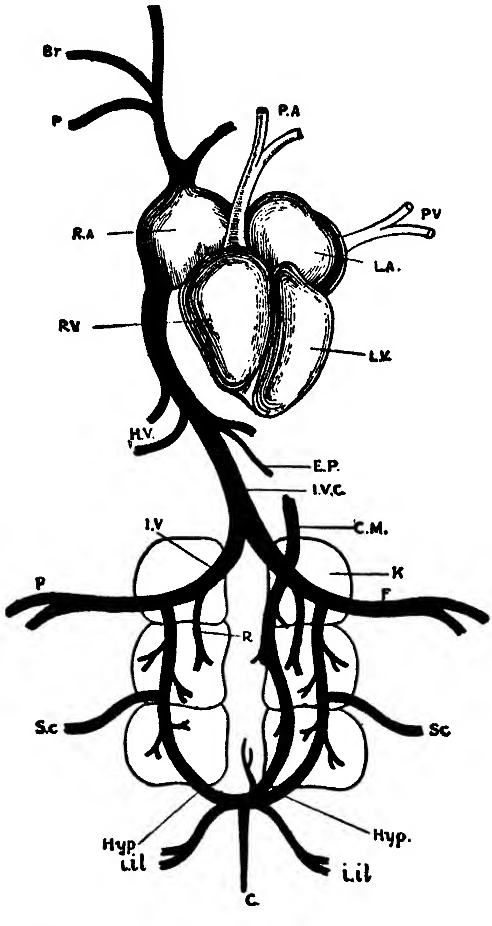


FIG. 23.20.—Heart and venous system of a pigeon.—From Thomson.

R.A., Right auricle ; *R.V.*, right ventricle ; *L.V.*, left ventricle ; *L.A.*, left auricle ; *P.V.*, pulmonary veins ; *P.A.*, pulmonary arteries ; *J.*, jugular ; *Br.*, brachial, and *P.*, pectoral joining to form the precaval vein ; *H.V.*, hepatic ; *E.P.*, epigastric ; *I.V.C.*, postcaval vein ; *C.M.*, coccygeo-mesenteric ; *I.V.*, iliac ; *F.*, femoral ; *R.*, renal ; *Sc.*, sciatic ; *Hyp.*, hypogastric or 'renal portal' ; *i.il.*, internal iliac ; *C.*, caudal ; *K.*, kidney.

hypogastrics arise in the following way. The little caudal vein forks into two branches, each of which runs through one of the kidneys as a hypogastric. Each hypogastric is much larger than the caudal of which it is a branch, because at the bifurcatio: another vein, the coccygeo-mesenteric from the cloaca and large

intestine, joins the caudal, and immediately after it has separated from its fellow the hypogastric receives an internal iliac vein. In its course through the kidney it receives several small renal veins and a sciatic. There is a small renal portal system, the femorals giving a few branches to the kidneys. A hepatic portal system exists as usual. A vein, usually known as the epigastric, takes blood from the great omentum, or sheet of fat which covers the abdominal viscera, to the left hepatic vein. It represents the anterior abdominal vein of the frog. There is much variation in the details of the vascular system of different species of birds.

EXCRETORY AND REPRODUCTIVE ORGANS

The kidneys are metanephric (pp. 629–31). They lie in the back under the sacrum as a pair of three-lobed bodies (Figs. 23.21, 23.22). From the hinder lobe of each a ureter runs back to the cloaca. There is no bladder. Nitrogen is excreted as uric acid, not urea. The urine is very concentrated and in the cloaca the

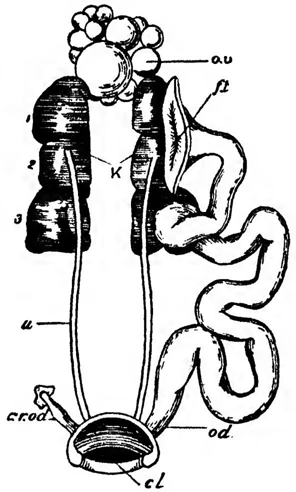


FIG. 23.21.—The urogenital organs of a female pigeon.—From Thomson.

K., Kidney (metanephros) with three lobes; *u.*, ureter; *cl.*, cloaca; *ov.*, ovary; *od.*, oviduct; *fl.*, funnel at end of oviduct, *r.r.od.*, rudimentary right oviduct.

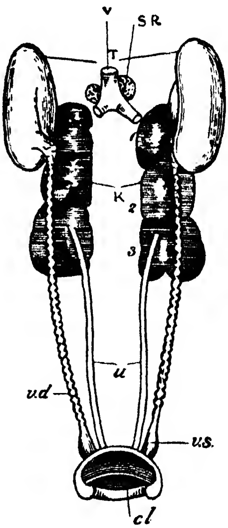


FIG. 23.22.—The urogenital organs of a male pigeon.—From Thomson.

T., Testes; *V.*, base of inferior vena cava; *S.R.*, suprarenal glands; *K.*, kidneys with three lobes (1, 2, 3); *u.*, ureter; *v.d.*, vas deferens; *v.s.*, seminal vesicle; *cl.*, cloaca.

uric acid is precipitated and the water, with some salts, is saved for the body by reabsorption as in the rectum of the cockroach. There is some tubule excretion from the renal portals. The sexes are separate. The testes lie in front of the kidneys. From each of them the vas deferens, corresponding to the Wolffian duct of the dogfish and frog, runs back on the outer side of the ureter to end in a small swelling or seminal vesicle which opens into the cloaca. When it is full of ripe sperms the vas deferens is slightly convoluted. There being no penis (though some birds, such as ducks, have one made of two incompletely joined halves) the semen is passed in coition by the cloaca of the male being closely apposed to that of the female. The adult pigeon has only one ovary, that of the right side having atrophied early in life. The right oviduct also atrophies, but a small vestige remains attached to the cloaca. The ovary is covered with follicles which contain ova in various stages of ripeness. The oviduct is a wide, twisted tube, thin-walled in front and thick behind, opening into the body cavity by a long funnel just behind the ovary. When the ova are ripe they are shed into the body cavity and immediately caught by the opening of the oviduct. Each ovum is a large, round, yellow body which becomes the 'yolk' of the egg (Fig. 28.19). It is a single gigantic cell, so full of yolk that the protoplasm is practically restricted to a small patch at one side, containing the nucleus. It is fertilised in the thin region of the oviduct, coated with white of egg in the first part of the thick region, and provided with a double membrane and a porous chalky shell in the hinder part. The eggs are hatched by the warmth of the body of the parents, who sit upon them in turns. The young, which emerge after sixteen days, are provided with a scanty yellow down and, unlike young chickens, are at first quite helpless, with closed eyelids. They are fed by their parents with a cheesy fluid known as 'pigeon's milk', rich in protein and fat, which is formed by the breaking down of the epithelium of the crop. They are fledged at the end of three weeks, and after a few days' education in flight by their parents go out into the world for themselves. Birds are remarkable for their elaborate sexual ritual and courtship, which are associated with marked seasonal variations in size of the gonads, and with the activity of the pituitary gland. They also show a very high degree of parental care, the young being fed and defended until they are as large as their parents.

NERVOUS SYSTEM AND SENSE ORGANS

The cerebral hemispheres of the brain (Fig. 23.23) are large, smooth, and rounded. The roofs of the lateral ventricles are relatively thin, though nervous, but the corpora striata are large ; with this development is connected the elaborate but stereotyped behaviour of birds. This is in large part based on a number of fixed patterns of response, or instincts, but that considerable learning is possible is shown by the rapid spread of such new and peculiar habits as the opening of milk bottles by tits. The olfactory

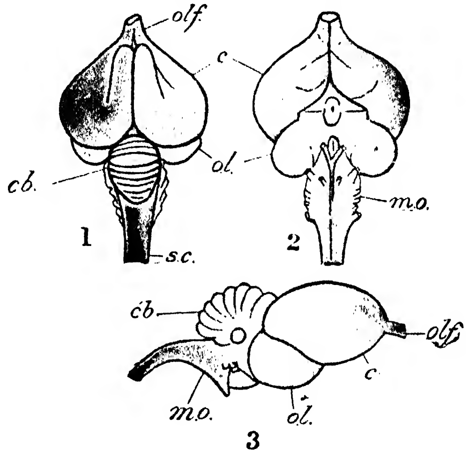


FIG. 23.23.—The brain of a pigeon.—From Thomson.

(1) **Dorsal**, (2) **ventral**, and (3) side view. *c.*, Cerebral hemispheres ; *cb.* cerebellum ; *m.o.*, **medulla oblongata** *o.l.*, optic lobes ; *olf.*, olfactory lobes ; *s.c.*, spinal cord.

lobes are very small. The cerebellum and cerebrum meet over the thalamencephalon, thrusting the round, hollow optic lobes to the sides. The cerebellum is ridged transversely. There are twelve cranial nerves, corresponding to those of the rabbit (p. 461). The sense of smell is poorly developed in most birds, though good in the kiwi (*Apteryx*) and some others. Hearing is acute, the labyrinth possessing the organ known as the cochlea which was quite rudimentary in the frog. Sight is very keen, and the eye is remarkable for the presence of a vascular pigmented organ, known as the pecten, which protrudes into the vitreous humour from the ' blind spot ' where the optic nerve enters. This is possibly concerned with the appreciation of movement. There is a high density of cones, and two special concentrations of them, or

foveæ (p. 464). The visual acuity of the general surface of the retina of most birds is probably as good as that of the fovea of man.

BIRDS AND REPTILES

Warm-blooded though they are, birds are more akin to reptiles than to mammals. This is expressed in many details of their

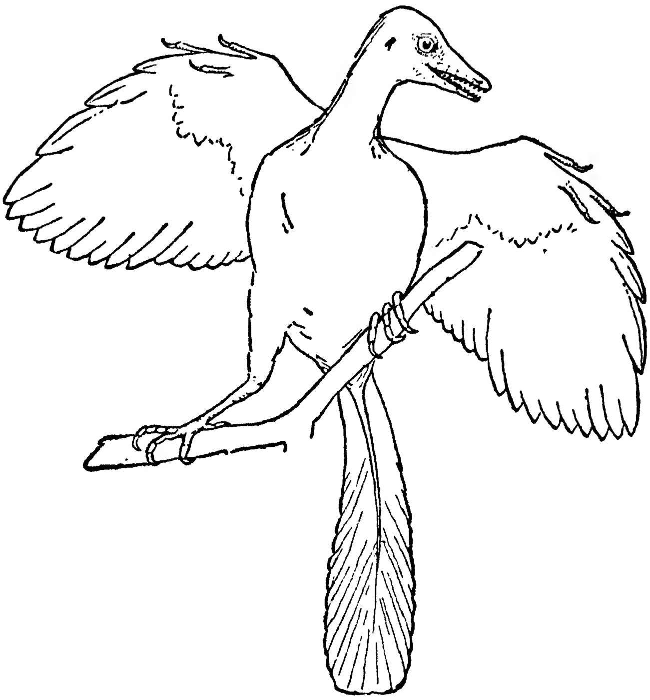


FIG. 23.24.—Restoration of *Archæopteryx*.—From Thomson, after Pycraft.
The figure shows the teeth in the jaws, hints of the biserial tail feathers, and the three clawed digits on the outstretched wings which are seen from the ventral aspect.

anatomy—the structure and articulation of the lower jaw, various other features of the skull, the ankle joint, the organs of reproduction, the carriage of oxygenated blood by the right systemic arch, the nucleated red blood corpuscles, the scaly legs, etc. An interesting link between birds and reptiles is the extinct *Archæopteryx* (Fig. 23.24), of which there are three specimens from the Upper Jurassic. These creatures were, as far as is known, birds in all essential features, but had, like a reptile, teeth, free fingers on the hand, and many vertebræ in the long, flexible tail.

24

THE RABBIT

THE rabbit, *Oryctolagus cuniculus* (=*Lepus cuniculus*), was introduced into Britain by man from its original home in the countries at the western end of the Mediterranean. Thence it has spread or been carried by man throughout most of Europe and into various other parts of the world, where its adaptability and great fertility have enabled it to thrive to such an extent, that often, as notably in Australia, it has become a serious nuisance. It is herbivorous, feeding mainly in early morning and late afternoon. It is gregarious, and lives, when not feeding, either in burrows which it digs for itself or in runs in thick vegetation. It is readily domesticated, and various fancy races have been produced by breeders.

The rabbit is studied as an example of the vertebrates, and also of the class Mammalia. Much of the description which follows will apply to the rat or guinea-pig, which are other mammals commonly dissected, some to the frog and bird, which agree with the mammals in being tetrapods, i.e. vertebrates with four limbs built on the pentadactyl plan (p. 415), and a little to the dogfish, which shows the fundamental vertebrate plan very clearly but differs widely from the mammals in the disposition and structure of the parts.

EXTERNAL FEATURES

The rabbit is covered with fur, which in the wild race is usually of an inconspicuous, tawny-grey colour known as agouti ; the under side of the short, upright tail is white. Black, sandy and other colour varieties are common. The head is separated from the trunk by a distinct neck, and the long external earflaps or pinnæ are conspicuous. The eyes have movable upper and lower lids with a few eyelashes, and a small third eyelid lies as a white membrane in the inner corner and is used in cleaning the cornea. This eyelid is rudimentary in man. The nostrils are two oblique slits at the end of the snout, and lead internally into the pharynx. The upper lip is a ' hare lip ', cleft in the middle, the cleft being continuous with the nostrils and exposing the great front teeth.

On the sides of the snout and round the eyes there are strong tactile hairs or vibrissæ which correspond to the so-called 'whiskers' of the cat. The anus and urogenital openings are separate, the latter in front of the former, in the male on the end of a penis, in the female within a slit-like vulva which contains in front a small clitoris corresponding to the penis. Beside the penis in the male lie the scrotal sacs, into which the testes of the adult descend, but there is no hanging scrotum. Along the breast and belly of the female there are four or five pairs of teats on which open the milk glands of the mammæ. At the sides of the anus are a pair of hairless depressions, into which open the ducts of the perineal glands, to whose secretion is due the peculiar smell of the rabbit.

LIMBS

There are two pairs of limbs (Fig. 24.1), of a type called pentadactyl, with a number of jointed segments. In the fore-limb or arm the proximal segment (that nearest the body) is the upper arm or brachium ; articulated with this is the fore-arm or antebrachium, and distally (farthest from the body) is the forefoot or hand or manus. The junction between the ante-brachium and the manus is made by the wrist or carpus ; beyond this is the palm or metacarpus, and finally there are the fingers or digits, each made up of a number of phalanges. The first (inner) of these is distinguished as the thumb or pollex. As the English names for the fore-limb and its parts, which are those for the arm of man, are not entirely appropriate to the fore-leg of a rabbit or the wing of a bird, it is generally better to use the alternative Latin names, where the absurdity, though still present, is shrouded in the decent obscurity of a learned language. The hind-limb or leg has corresponding parts. The proximal segment is the thigh or femur, though the second word is best avoided in this sense, as it is more commonly used for the contained bone, then comes the shank or crus, and distally the foot or pes. The parts of the foot are the ankle or tarsus, the instep or metatarsus, and the toes or digits, made up of phalanges. The first digit (absent from the rabbit) is the big toe or hallux. The lower side of the foot is the plantar surface or sole, that of the hand the palm, but the rabbit is digitigrade, running with only the tips of the digits on the ground. The digits of both fore

and hind-limbs end in claws. An animal such as man, who places the sole of the foot on the ground, is called plantigrade.

The skin, which is described in more detail in Chapter 26, is covered with a stratified epidermis. There are no scales, but

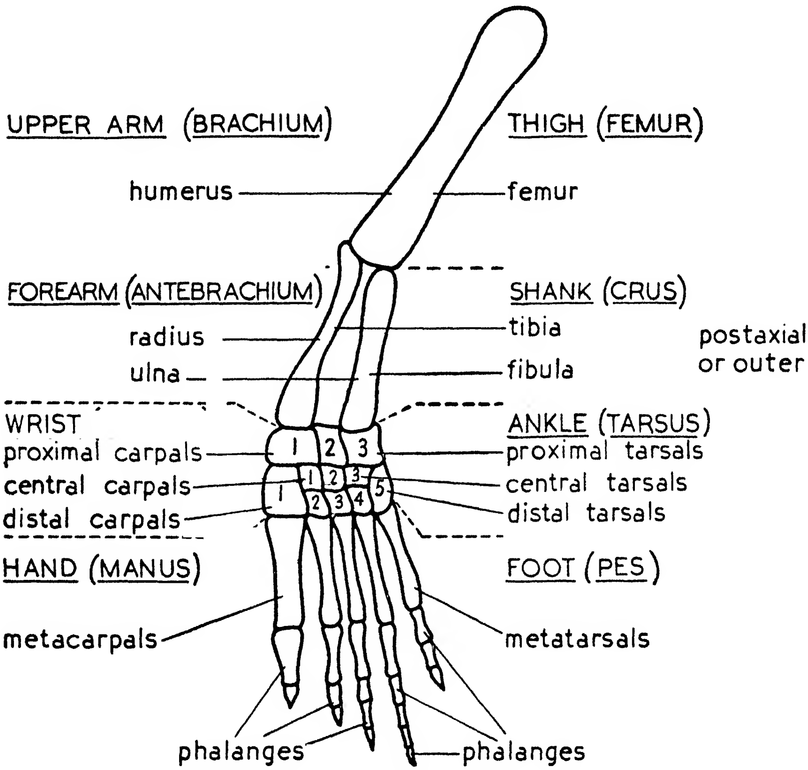


FIG. 24.1.—A diagram of a pentadactyl limb (cheiropterygium). Names of the fore-limb on the left, of the hind-limb on the right. Metacarpals and metatarsals are together called metapodials.

cellular outgrowths of the epidermis form hairs, which are peculiar to the Mammalia. The skin also contains sweat or sudorific glands and grease or sebaceous glands which secrete an oily substance into the hair follicles.

INTERNAL STRUCTURE

The muscles of the adult rabbit show little trace of the segmentation which they have in the early stages of development.

In the trunk (Fig. 24.2) they are arranged in the form of a tube, which encloses a large space, the body cavity or cœlom. On the dorsal surface this tube is very much thicker than elsewhere, and the muscles here surround the backbone and the limb girdles. The cœlom is lined by a membrane, the peritoneum, which is continued over the surface of the intestine and other organs (the viscera) which the cœlom contains. The viscera are in fact not strictly in the cœlom, but slung from its roof by folds in the lining of the roof itself. As the gut comes to be very much longer than the cœlom the folds are very difficult to follow in the adult animal. Those which sling the stomach, liver, duodenum and spleen are called omenta, and those supporting the rest of the gut mesenteries. The cœlom is divided into two by a vertical muscular partition, the midriff or diaphragm, which separates off from the peritoneal cavity of the abdomen a chest or thorax in the breast

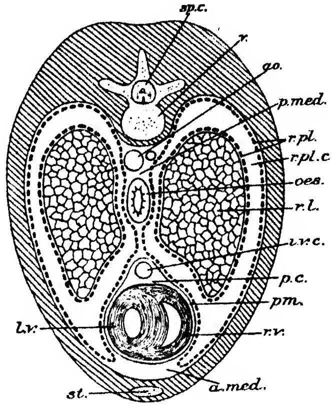


FIG. 24.2.—A diagram of a transverse section through the thorax of a rabbit.

a.med., Ventral part of mediastinum; *ao.*, aorta; *i.v.c.*, inferior vena cava; *l.v.*, left ventricle; *œs.*, œsophagus; *p.c.*, pericardial cavity; *p.med.*, dorsal part of mediastinum; *pm.*, pericardium; *r.l.*, right lung; *r.pl.*, right pleura; *r.pl.c.*, right pleural cavity; *r.v.*, right ventricle; *sp.c.*, spinal cord; *st.*, sternum; *v.*, vertebra.

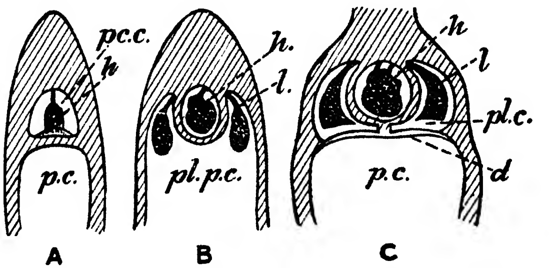


FIG. 24.3.—A diagram of the perivisceral cœlom in transverse section: *A*, of the dogfish; B, of the frog; *C*, of the rabbit or man.

d., Diaphragm; *h.*, heart; *l.*, lung; *p.c.*, peritoneal cavity; *pl.c.*, pleural cavity; *pl.p.c.*, pleuroperitoneal cavity; *pc.c.*, pericardial cavity.

region, where lies the pericardium, with on each side a pleural cavity, into which the lung of its side projects. The lining of

each pleural cavity is known as a pleura, and of course covers the lung as well as the inside of the thorax. The heart in its pericardium does not lie free in the cavity of the chest, as that of the frog does in the anterior part of the pleuroperitoneal cavity, but is fastened to the dorsal and ventral walls of the thorax by a double sheet of membrane, each sheet forming the inner wall of a pleural cavity. Between the sheets is a lymph-space known as the mediastinum. In the dorsal part of this space lie the aorta, certain other blood vessels, and the œsophagus; its middle part is quite filled by the pericardium, with which its walls fuse; and in its ventral part lies the thymus.

SKELETON

The skeleton of the rabbit has the general features which are characteristic of vertebrates. It is predominantly an endo-skeleton, situated internally, and is developed internally in mesoderm (p. 186). For descriptive purposes it is divided into two parts, the axial skeleton running the length of the body, and the appendicular skeleton attached to this. The axial skeleton consists of the skull, and the backbone or vertebral column extending to the end of the tail. In the thorax there are, attached to the vertebral column, ribs, which meet a ventral axial piece, the breast-bone or sternum. The separate segments of the backbone are vertebræ. The appendicular skeleton consists of two hoops of bone, the limb-girdles, to which the skeletons of the limbs are attached. The structure of a joint or articulation, where one part of the skeleton is movable on another part, is shown in Fig. 24.4. The synovial capsule is a fibrous bag containing a watery fluid, the synovia, the whole forming a spring and a lubricant. The very low coefficient of friction of surfaces of articular cartilage (0·01–0·02) is maintained by the seepage of

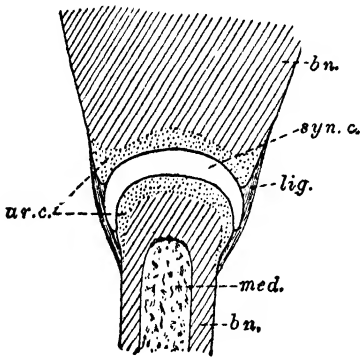


FIG. 24.4.—A diagram to illustrate the structure of 'perfect' joints.

ar.c., Articular cartilage; *bn.*, bone; *lig.*, ligament; *med.*, medulla or marrow; *syn.c.*, synovial capsule.

extracellular fluid to give the same sort of effect as a closed-cell sponge. In imperfect joints the synovial capsule is replaced by a layer of cartilage or fibrous tissue, and the amount of movement is small. The movement of the joint is brought about by the contraction of muscles; the end of a muscle attached to a relatively fixed point is its origin, that attached to a movable

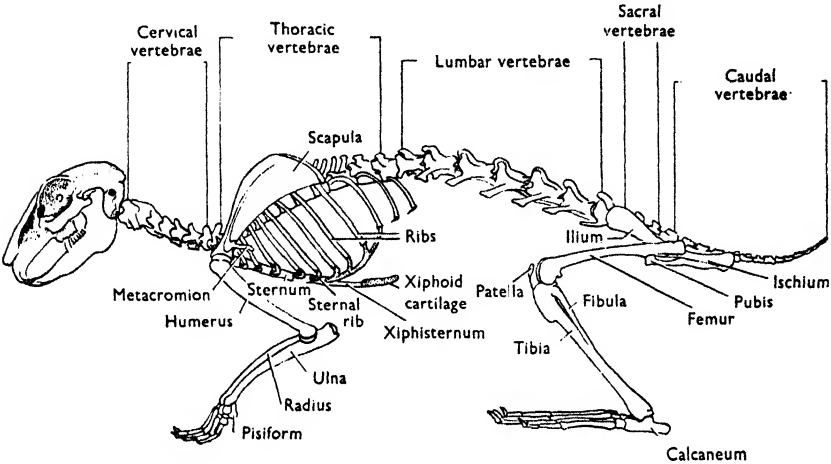


FIG. 24.5.—Rabbit. The skeleton from the left side. The limbs and ribs of the right side are not shown. × 0·3.

one its insertion. Muscles are fastened to bones by means of tendons.

In the embryo the skeleton is first formed in cartilage or gristle (p. 520), but for the most part this is replaced by the harder and more durable bone (p. 521). Cartilage persists on the surfaces of joints and in a few other places. In the skull and the shoulder girdle there are, in addition to the cartilage bones formed in (but not from) cartilage, other sets called membrane bones. These are really part of an exoskeleton which has sunk inwards from the skin. Small bones are also formed in other tissues.

BACKBONE

Each vertebra (Fig. 24.6) is entirely bony and consists of a body or centrum with above it a neural arch which encloses a vertebral foramen, surmounted by a neural spine or spinous process. Each arch bears in front an upward-facing facet or anterior articular process or prezygapophysis, and behind a downward-facing

posterior articular process or postzygapophysis which fits on to the corresponding prezygapophysis of the next vertebra, while at the side a transverse process projects, and at each end there is an intervertebral notch for the passage of a spinal nerve, the adjacent notches of two vertebræ enclosing an intervertebral foramen.

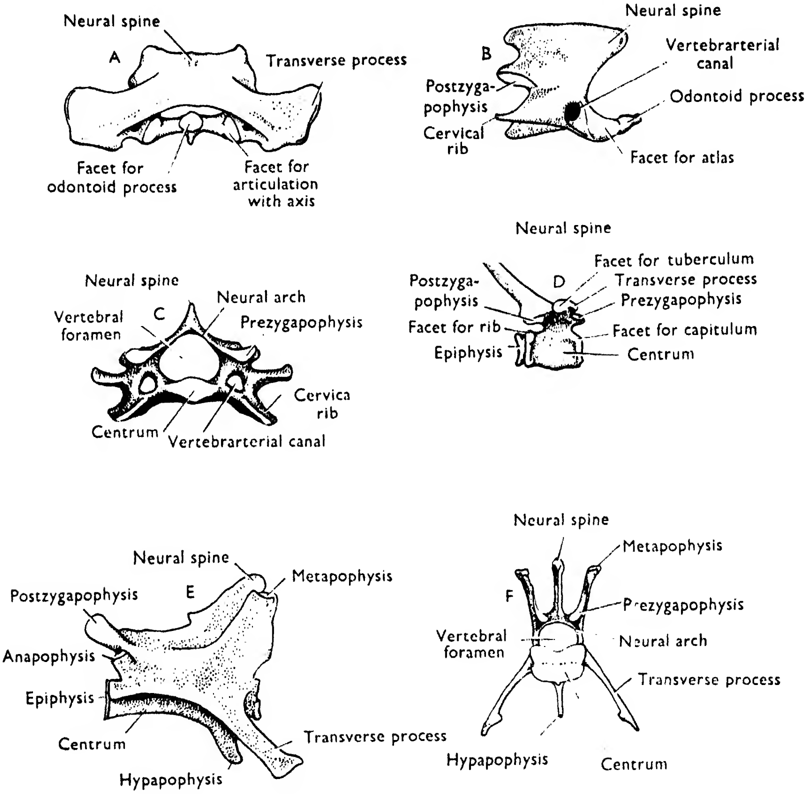


FIG. 24.6.—Vertebræ of rabbit. *A*, atlas, from above ; *B*, axis, from the right ; *C*, fourth cervical, from in front ; *D*, fourth thoracic, from the right ; *E*, second lumbar, from the right ; *F*, second lumbar, from in front. × 1.

Each end of each centrum, with the exception of the first two, is flat, a shape known as amphiplatyan, and against it in the young rabbit is a thin bony disc or epiphysis, which fuses with it when growth is complete. The general characters of the vertebræ of the rabbit may be well studied in that known as the second lumbar (see below), but this and the others show many peculiarities. The backbone is divided into five sections, the neck or

cervical, chest or thoracic, loin or lumbar, hip or sacral, and tail or caudal regions. In the cervical region there are in all mammals seven vertebræ, which may be recognised by the fact that apparently each of the transverse processes is pierced by an opening (its foramen) : there is thus formed on each side a vertebrarterial canal, through which pass the vertebral artery and

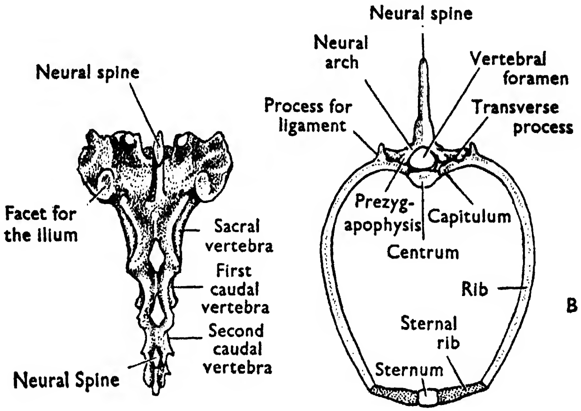


FIG. 24.7.—Rabbit. *A*, the sacrum, from above : × 1 ; *B*, a segment of the skeleton of the thorax, from in front. × 0·5.

vein. This is due to the fusion with the vertebræ of short cervical ribs in such a way as to constitute a compound ' transverse process ' which encloses a space. The first vertebra, known as the atlas, is ring-shaped, with a very large vertebral foramen and no centrum. The ring is divided by a ligament into an upper part, through which the spinal cord passes, and a lower part, into which fits a peg, the odontoid process, projecting forward from the centrum of the second vertebra. This peg represents the centrum of the atlas removed from it and fused with the vertebra behind. The transverse processes of the atlas are very broad, and the front side of the vertebra has two very large articular surfaces for the occipital condyles of the skull. The second vertebra is known as the axis. It has a long, crest-like neural spine and bears the odontoid process. The remaining cervical vertebræ are short and broad, with low neural spines, but that of the seventh is longer than the others. The thoracic region contains twelve or thirteen vertebræ, which are characterised by bearing movably articulated ribs. The neural spines are tall, the transverse processes short and stout, and each, in the first

nine vertebræ, provided on the under side with a facet or ' costal pit ' for articulation with the tubercle of a rib, presently to be described. The front end of the centrum (in the first nine the hinder end also) bears on each side a facet for the head of the rib. The hinder vertebræ of this set gradually become more like those of the lumbar region. These are usually seven in number. They are characterised by their large size and the great development of their processes, the prezygapophysis being borne upon the inner side of a large metapophysis and the hinder intervertebral notch being overhung by a small anapophysis. In the first two the centrum bears a median ventral hypapophysis. The lumbar vertebræ have no ribs. The sacral vertebræ are those to which the hip girdle is attached ; there is usually only one, but sometimes two are found. These vertebræ are large and bear at the sides a pair of wing-like expansions, which support the hip girdle and are probably ribs fused with the vertebra. A certain number of the succeeding vertebræ are fused with the true sacral vertebra, the whole mass being known as the sacrum. The caudal region contains about eighteen vertebræ, of which the first three or four are fused with the sacral. They grow smaller from before backwards, losing their processes and becoming degenerate.

RIBS AND BREASTBONE

The ribs are present as independent elements only in the thoracic region. They are curved, bony rods, articulated with the vertebræ. Those of the first nine pairs are connected at their lower ends with the breastbone by bars of calcified cartilage known as their sternal portions or as sternal ribs. The end which articulates with the vertebra has a knob known as the head or capitulum. The first nine pairs have a second facet on the dorsal side at a short distance beyond the head. This is for articulation with the transverse process of the vertebra ; immediately beyond it, for the attachment of ligaments, is a short projection, together with which it forms the tuberculum. The sternal portions of the first seven pairs articulate directly with the sternum ; those of the eighth and ninth are connected with the ribs in front of them. The last three pairs have no sternal portions and no tubercula. The breastbone or sternum is a long, narrow rod, divided into segments, sometimes called sternebræ, and lying in the mid-ventral line of the thorax. The first segment is the manubrium.

It is the largest and is flattened from side to side. Behind it come four segments of equal size, then a very short segment, and finally the xiphoid process or xiphisternum, a long, slender rod, which bears behind a horizontal plate of cartilage. The first pair of ribs articulate with the sides of the manubrium, and the succeeding six pairs at the junctions between the segments.

THE SKULL OF THE DOG

The details of the skull of the rabbit are difficult to make out, and it is much better to study first that of the dog (Figs. 24.8, 24.9), on which the following description is based. The skull of vertebrates has two parts, a dorsal and a ventral, but in mammals the latter, which is well seen in the dogfish (p. 316) is practically reduced to the jaws. The dorsal part consists of a cranium or brain box surrounding the brain, and two pairs of sense capsules, the auditory capsules posterolateral to the cranium, and the nasal capsules in front. The optic capsules, which are present in the embryo, are reduced in the adult to some cartilage in the sclerotic coat of the eye. In adult mammals almost the whole skull is bony. The cartilaginous cranium is ossified to form a number of bones which are joined to each other by jagged edges called sutures. At the posterior end, surrounding the foramen magnum, the hole through which the spinal cord passes to merge with the brain, are four, a basioccipital below, a supraoccipital above, and an exoccipital on each side. The exoccipitals make two knobs, the occipital condyles, which articulate with the first vertebra ; a small part of each condyle is formed from the basioccipital. In front of the basioccipital the floor of the cranium is made by the basisphenoid, a rhomboid-shaped bone with the narrow side anterior ; its upper surface is thickened in the middle, and in the thickening is a depression, the sella turcica, in which lies the pituitary body (p. 470). Arising from the basisphenoid on each side is an alisphenoid, which here forms the side walls of the cranium. In front of the basisphenoid is a narrow presphenoid, and on each side of this an orbitosphenoid, which continues the side wall of the cranium. Presphenoid and orbitosphenoids are not recognisable as separate bones. The front wall of the skull is made by the cribriform plate, a wall of bone pierced with many holes for the olfactory nerve ; it is part of the mesethmoid, which also has a median vertical extension forwards, the nasal septum.

The cartilage bones leave the roof of the brain uncovered. This gap is filled in with membrane bones: a pair of large parietals above the alisphenoids, a pair of large frontals above the orbito-sphenoids, a pair of small lacrimals below and in front of the

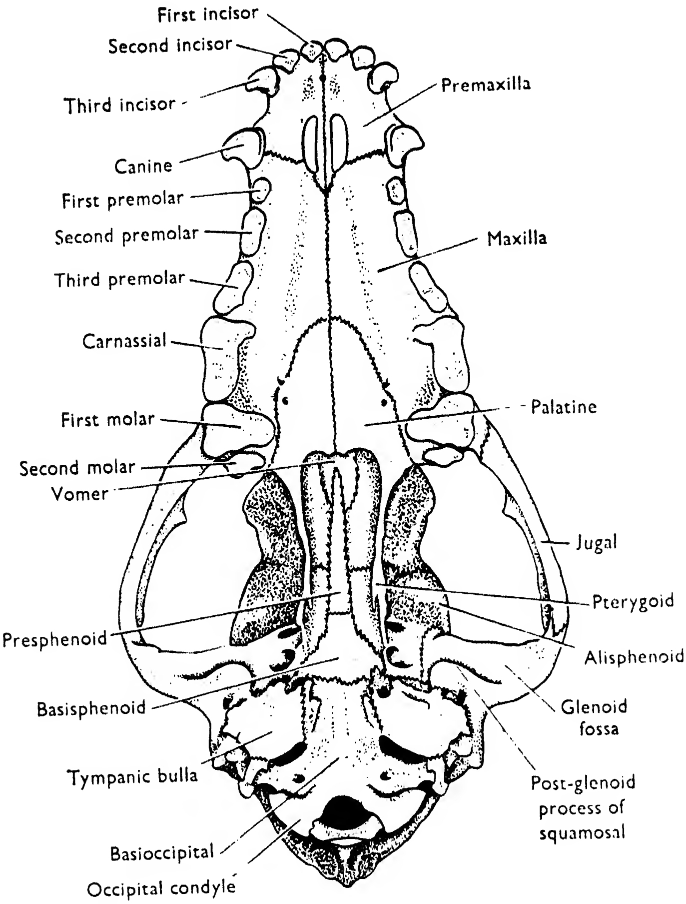


FIG. 24.8.—The skull of a dog, ventral view. × 0·5

frontals, and a small unpaired interparietal above the supra-occipital. Part of the wall of the skull between the exoccipital and the alisphenoid is made by the auditory capsule. It is sometimes helpful to learn the main bones of the cranium as three rings, with no distinction of cartilage and membrane bones. The occipital ring consists of supra-, basi-, and

exoccipitals; the parietal ring of basi- and alisphenoids and parietals; and the frontal ring of pre- and orbitosphenoids and frontals. The interparietal and parietals are raised into a median sagittal crest, to which muscles are attached. The frontals are pressed inwards below to make two hollows, the orbits, into which fit the eyes, and on its upper edge each frontal has a conspicuous postorbital process which juts out over and behind the eye. The orbitosphenoid may always be recognised by the

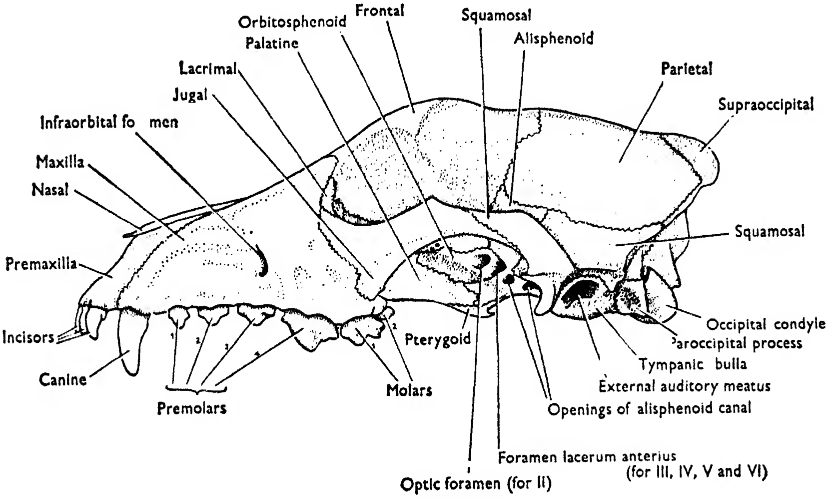


FIG. 24.9.—The skull of a dog, from the left side and tilted slightly away from the observer. × 0·3.

fact that it entirely surrounds the optic foramen, which is the most anterior large hole in the orbit. The alisphenoid, which is behind the orbitosphenoid, may be recognised because it bears near its surface a conspicuous tunnel, the alisphenoid canal, through which a seeker may be passed from one end to the other without going into the cranial cavity.

As we have seen, the auditory capsule makes part of the side wall of the brain-box. It ossifies from three centres, but in the adult only a single cartilage bone, the periotic or petrosal, can be recognised. Most of it, which encloses the inner ear, can only be seen in a sectioned skull, but a small part, which bears a projection, the mastoid process, is visible externally. The membrane bone of the auditory capsule is the squamosal, one of the

largest bones in the skull, which completes the side wall between alisphenoid and the exoccipital. It has a large outwardly and forwardly projecting zygomatic process; the upper part of this forms part of the zygomatic arch, a half-hoop of bone which runs outside the jaw muscles below the eye, and the lower forms a cylindrical hollow for articulating with the lower jaw. Associated with the auditory capsule of mammals are some other bones, which, although they originally belonged to the ventral part of the skull, have become intimately associated with the ear. The tympanic is visible on the outside, between the mastoid process and the squamosal, as a flask-shaped bulla. Inside the lower end of the neck of this is a ring, where in life the ear drum is fixed; the neck leads up from this to the surface of the head, forming a passage, the external auditory meatus. The body of the bulla encloses the tympanic cavity, the posterior wall of this being made by the petrosal. In this are two gaps, the fenestra ovalis and fenestra rotunda (p. 468) and from the former of these a chain of three ear ossicles runs to the ear drum. These are, from the drum inwards, the malleus, incus, and stapes.

The nasal capsule is partially ossified to form the front part of the mesethmoid, which we have already mentioned, but much cartilage remains. The surface of the nasal cavities is much increased by three pairs of thin, rolled cartilage bones known as turbinals. The membrane bones of the capsule are a pair of nasals, which form the roof of the nasal cavities, and a median vomer, which is formed from paired elements and has a forked vertical part partially enclosing the lower edge of the cartilaginous nasal septum, and lateral wings which separate the nasal cavities into upper olfactory chambers which are blind, and a lower nasal passage which opens posteriorly into the pharynx.

JAWS

The ventral part of the skull, consisting of the jaws and visceral arches, is much better seen in the dogfish, where it is reasonably complete. In mammals little is left of it but the jaws.

The cartilaginous upper jaw in the embryo is known as the palatopterygoquadrate bar, because in some lower vertebrates it becomes ossified to form three bones called palatine, pterygoid, and quadrate. In mammals, however, most of the cartilage breaks down and disappears, leaving bone only in the middle

and at the posterior end. The middle portion forms the alisphenoid, which we have already seen forming part of the side wall of the brain-box, and the posterior quadrate becomes the incus, one of the ear ossicles. The functional upper jaw is thus made entirely of membrane bones. The bone usually called pterygoid, but better called ectopterygoid to show that it is not the cartilage bone of that name, projects downwards as a triangular plate from the junction of the basisphenoid with the alisphenoid. In front of this the dermal palatine stretches forwards below and at the side of the presphenoid. Its anterior part is bent inwards and meets its fellow in the middle line, so that the narial passage is extended backwards and the internal nares open far back in the buccal cavity. The secondary roof to the

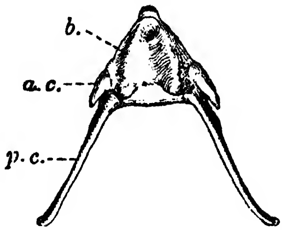


FIG. 24.10.—The hyoid bone of a rabbit, from above.

a.c., Base of the anterior cornu ; *b.*, body ; *p.c.*, posterior cornu.

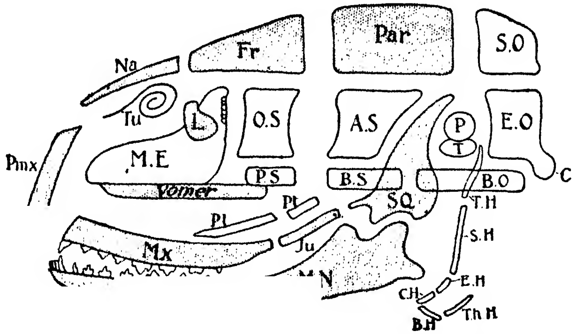


FIG. 24.11.—A diagram of the skull bones of a mammal (partly after Flower and Weber), the membrane bones shaded.

B.O., Basioccipital ; *E.O.*, exoccipital ; *C.*, condyle ; *S.O.*, supraoccipital ; *Par.*, parietal ; *Fr.*, frontal *Na.*, nasal ; *Pmx.*, premaxilla ; *M.E.*, mesethmoid ; *L.*, lacrimal ; *Tu.*, turbinal ; *P.S.*, presphenoid *O.S.*, orbitosphenoid ; *A.S.*, alisphenoid ; *B.S.*, basisphenoid ; *SQ.*, squamosal ; *P.*, periotic ; *T.*, tympanic ; *Pl.*, palatine ; *Pt.*, pterygoid ; *Mx.*, maxilla ; *Ju.*, jugal ; *T.H.*, tympanohyal ; *S.H.*, stylohyal *E.H.*, epihyal ; *C.H.*, ceratohyal ; *B.H.*, basihyal ; *Th.H.*, thyrohyal ; *vomer* ; *MN.*, dentary.

mouth formed by this plate of bone is called the false palate. In front of and outside this series of upper jaw bones is a second set. Running forward from the zygomatic process of the squamosal, and completing the zygomatic arch, is the malar or jugal. It joins in front a short zygomatic process from a large bone called the maxilla. This makes up most of the face, and joins the nasal,

lacrimal, and frontal above. Below, it continues the false palate made by the palatine, and meets its fellow in the middle line. In front of the maxilla is a smaller premaxilla, which completes the face and palate, surrounds, with the nasals, the external

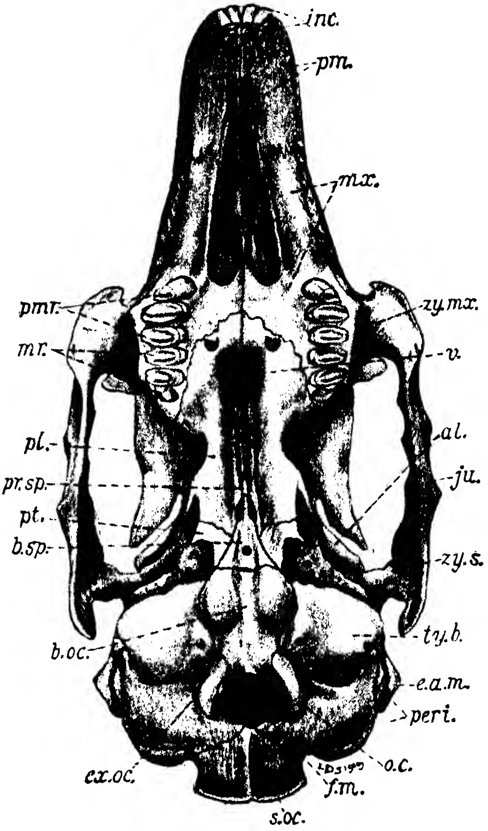


FIG. 24.12.—A ventral view of the skull of a rabbit.

a ., External process of the alisphenoid ; *b.oc.*, basioccipital ; *b.sp.*, basisphenoid ; *e.a.m.*, external auditory meatus ; *ex.oc.*, exoccipital ; *f.m.*, foramen magnum ; *inc.*, incisors ; *ju.*, jugal ; *mr.*, molars ; *mx.*, maxilla ; *oc.*, occipital condyle ; *peri.*, periotic ; *pl.*, palatine ; *pm.*, premaxilla ; *pmr.*, premolars ; *pr.sp.*, presphenoid ; *pt.*, pterygoid ; *s.oc.*, supraoccipital ; *ty.b.*, tympanic bulla ; *v.*, vomer ; *zy.mx.*, zygomatic process of maxilla ; *zy.s.*. zygomatic process of squamosal.

nostrils, and meets its fellow in front and below. This type of jaw suspension, in which the upper jaw is intimately joined to the cranium, is called autostylic (p. 589).

The cartilaginous lower jaw, known as Meckel's cartilage, entirely disappears in the adult except for two posterior fragments of it which have become ossified as the malleus. It is

functionally replaced by a single membrane bone, the dentary. This is loosely sutured to its fellow in front, and posteriorly has three conspicuous processes: an ascending coronoid, to which the muscles which close the mouth are largely attached, an angular at the lower corner, and between these an articular. This last is shaped like a roller, and fits into the hollow in the

TABLE V

THE CHIEF FORAMINA OF THE SKULL OF THE DOG

Name	Position	Structures Transmitted
Incisive	Lower surface of premaxilla	Blood vessels and nerves (maxillary branch of trigeminal) to palate
Palatine	Two or more pairs in horizontal portion of palatine	Branches of maxillary branch of trigeminal nerve
Infraorbital	Maxilla, in front of orbit	Maxillary branch of trigeminal
Lacrimal	Lacrimal	Lacrimal duct
Sphenopalatine	Ascending plate of palatine	Entry of maxillary branch of trigeminal to face
Ethmoid	Orbit, between maxilla and palatine	Maxillary branch of trigeminal nerve and ethmoid artery
Lacunæ of cribriform plate	Mesethmoid	Olfactory nerve
Optic	Orbitosphenoid	Optic nerve
Lacerum anterius	Between orbitosphenoid and alisphenoid	Oculomotor, pathetic and abducent nerves, and ophthalmic branch of trigeminal
Rotundum	Alisphenoid	Maxillary branch of trigeminal
Ovale	Alisphenoid, behind and outside rotundum	Mandibular branch of trigeminal
Alisphenoid canal	Horizontal tunnel in alisphenoid	External carotid artery
Lacerum medium	Between alisphenoid and periotic	Internal carotid artery
Internal auditory meatus	Periotic	Facial and auditory nerves
Stylomastoid	Between bulla and mastoid	Facial nerve
Lacerum posterius	Between periotic and exoccipital	Glossopharyngeal, vagus and spinal accessory nerves, and internal jugular vein
Condylar	Exoccipital	Hypoglossal nerve
Magnum	Posterior end of skull	Spinal cord
Inferior dental	Inner surface of dentary	Mandibular branch of trigeminal nerve
Mental	Outer surface of dentary	Mandibular branch of trigeminal nerve, and dental artery

squamosal. The result of this type of articulation is that although the mouth can be widely opened it cannot be moved from side to side without dislocation. The remainder of the ventral part of the skull is represented by the hyoid apparatus, and some cartilages on the larynx (p. 444). The hyoid, which is below the tongue, is shown in Fig. 24.10.

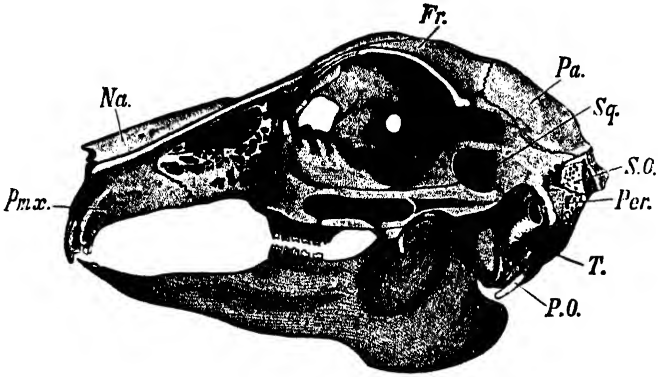


FIG. 24.13.—Side view of rabbit's skull.

Pmx., Premaxilla ; *Na.*, nasal ; *Fr.*, frontal *Pa.*, parietal ; *Sq.*, squamosal ; *S.O.*, supraoccipital *Per.*, periotic ; *T.*, tympanic (the reference line points to the bony external auditory meatus, beneath it lies the inflated bulla) ; *P.O.* paroccipital process.

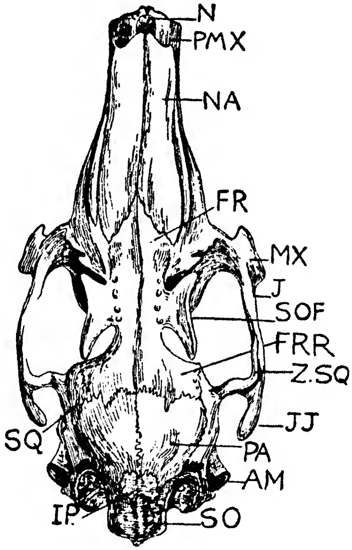


FIG. 24.14.—Upper surface of rabbit's skull.—From Thomson.

, Anterior nares ; *PMX.*, premaxilla ; *NA.*, nasal ; *FR.*, anterior part of frontal ; *MX.*, posterior part of maxilla; *J.*, anterior part of jugal ; *SOF.*, supraorbital process of frontal ; *FRR.*, posterior part of frontal ; *JJ.*, posterior end of jugal protruding below zygomatic portion of squamosal (*Z.SQ.*) ; *PA.*, parietal ; *A.M.*, external auditory meatus ; *SO.*, supraoccipital ; *IP.*, interparietal ; *SQ.*, squamosal.

The skull of the dog is complete, that is, there are no places where the brain is exposed, but it is pierced by several holes or foramina (singular foramen) for the passage of nerves and other structures, some of the more important of these are shown in Figs. 24.8 and 24.9, and in Table V.

The teeth are described more fully below, but it is appropriate here to give their names, since these depend on the bones which bear them. In mammals the teeth are thecodont, or embedded in sockets in the bone, and heterodont, or of a number of different shapes. In the upper jaw those borne in the premaxilla are incisors ; in the premaxilla-maxilla suture or immediately behind it there is on each side a single canine or eye-tooth ; all the rest of the teeth are borne by the maxilla, and are cheek teeth or grinders. In the lower jaw, where all the teeth are necessarily borne in the dentary, the same names are given to the teeth as to those which bite against them, except that the lower canine is that which bites just in front of the upper.

The skull of the cat is closely similar to that of the dog except that the facial region is much shorter and there are differences in the teeth ; the mastoid process of the periotic is not exposed, so that the exoccipital is in contact with the tympanic bulla. In the rabbit's skull the pterygoid region is difficult to make out ; the orbit and maxillæ are incomplete (fenestrated) ; and the zygomatic arch and supraoccipital have peculiar shapes (Figs. 24.13, 24.14).

LIMBS

The appendicular skeleton consists of two paired girdles, the shoulder or pectoral girdle supporting the fore-limbs, and the hip or pelvic girdle supporting the hind-limbs. Formed of cartilage in the embryo, they consist almost entirely of cartilage bone in the adult.

The shoulder girdle (Fig. 24.15) practically consists of one bone, the scapula, on each side. This is a flat, triangular structure, with the apex directed downwards and forwards, and bears a prominent external ridge or spine, which at its lower end becomes free as an acromion with a long, backward metacromion. At the apex is the shallow glenoid cavity for the humerus, in front of which a small hook or coracoid process represents the coracoid, which is a separate bone in the frog. Along the convex dorsal border lies

a narrow cartilaginous suprascapula. The clavicle is a slender, curved membrane bone, lying in a ligament between the acromion and the sternum. In mammals which move the forearm freely, as in man (Fig. 27.16), it is well developed and articulates with acromion and sternum.

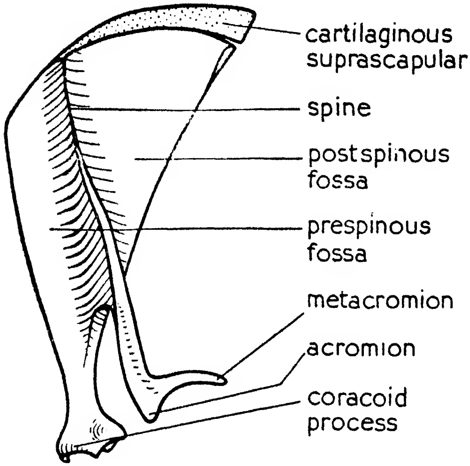


FIG. 24.15.—Left scapula of rabbit, outer (lateral) view. × 1.

The hip girdle (Fig. 24.16) is large, and each of its halves is known as an os innominatum or os coxæ. With the sacrum it forms a ring called the pelvis. In each os coxæ may be recognised a large dorsal ilium articulated with the sacrum, a posterior ischium, and a smaller, ventral and anterior pubis which unites with its fellow in a symphysis or fusion. The ischium and pubis are separated by a large obturator foramen, above and below which they meet. Above the obturator foramen all three parts of the os innominatum are continuous around the acetabulum, a hollow into which the head of the femur fits.

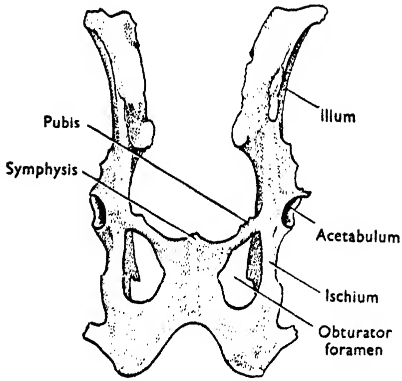


FIG. 24.16.—The pelvic girdle of a rabbit, from below. × 0·5.

The limbs contain bones for each of their segments ; a humerus in the brachium and a femur in the thigh ; a radius and an ulna in the forearm and a tibia and a fibula in the shank ; several carpals in the wrist and tarsals in the ankle ; metacarpals in the metacarpus and metatarsals in the metatarsus ; and a bone, not distinguished by name, in each phalanx of each digit (Fig. 24.1). The nomenclature of the carpals and tarsals is confused and difficult, and this

and other points about the limb skeleton are discussed more fully on page 562.

The limbs of tetrapods originally stuck out horizontally at

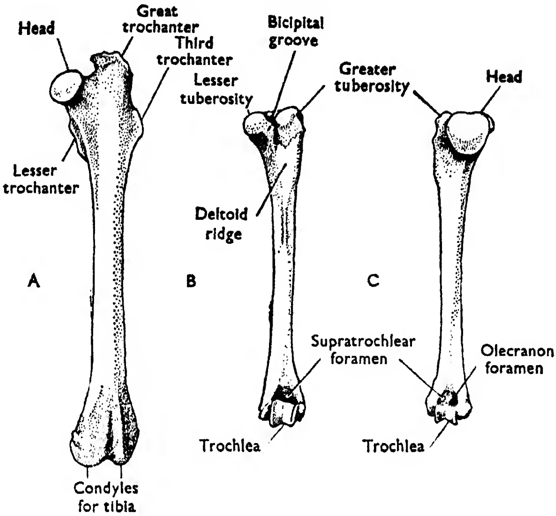


FIG. 24.17.—Rabbit. *A*, The left femur, from in front ; *B*, the left humerus, from in front ; *C*, the left humerus, from behind. × 0·5

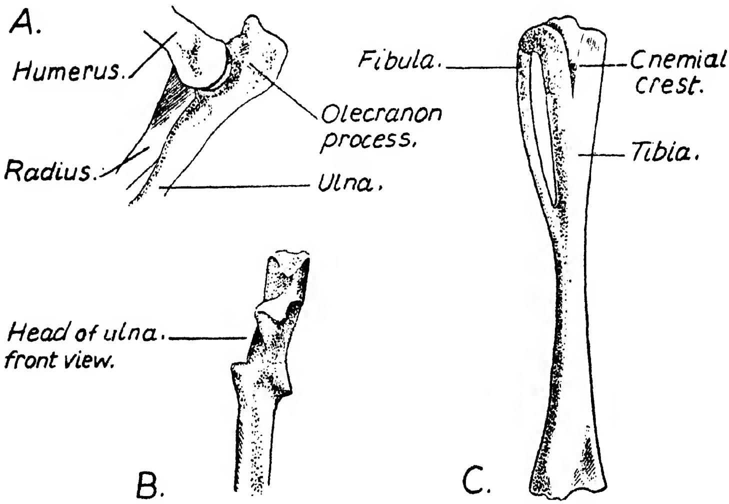


FIG. 24.18.—Rabbit. *A*, Elbow joint of left fore-limb, outer view ; *B*, head of right ulna, from in front ; *C*, right tibia, from in front. × 1.

right angles to the body, and the surface which in the rabbit has come to be inner, and in man ventral and anterior, is best known as preaxial; it is that which bears the radius and the thumb. The parts of the chief bones are shown in Figs. 24.17 to 24.19.

In the forearm the radius and ulna are distinct but not movable upon one another, the radius lying in front of the ulna. In man the

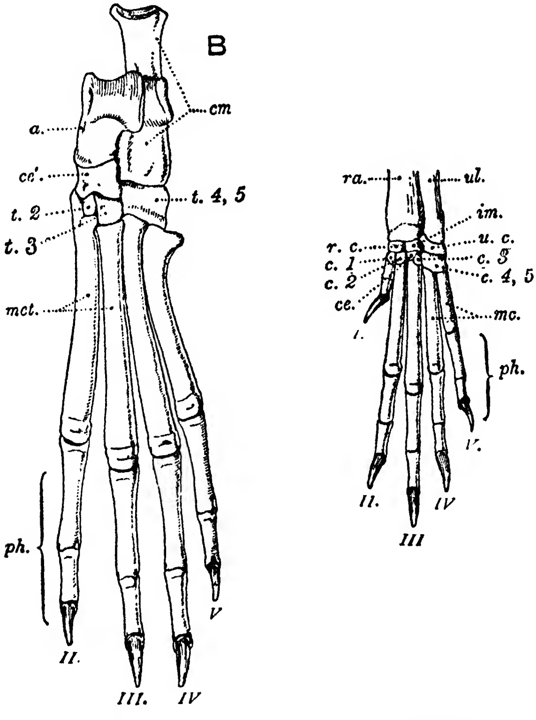


FIG. 24.19.—The skeleton of the left fore- and hind-feet of a rabbit. *A*, Fore-foot ; *B*, hind-foot.

a., Tibiale ; *c.*1, first distal carpal or trapezium ; *c.*2, second distal carpal or trapezoid ; *c.*3, third distal carpal or magnum ; *c.*4, 5, fused fourth and fifth distal carpals or unciform ; *ce.*, centrale ; *ce'.*, centrale of hind-foot ; *cm.*, fibulare ; *im.*, intermedium ; *mc.*, metacarpals ; *met.*, metatarsals ; *ph.*, phalanges ; *ra.*, lower end of radius with its epiphysis ; *r.c.*, radiale ; *t.*2, second distal tarsal or mesocuneiform ; *t.*3 third distal tarsal or ectocuneiform; *t.*4, 5, fused fourth and fifth distal tarsals or cuboid; *u.c.*, ulnare ; *ul.*, lower end of ulnar with its epiphysis ; *I.–V.*, digits.

lower end of the radius rotates round the ulna, so that the former lies in front of and obliquely across the latter when the palm faces downwards, but parallel with and outside it when the palm is turned upwards. The position in which the palm is downwards is known as pronation, that in which it is upwards as supination. In the frog the limb is fixed half-way towards pronation ; in the rabbit it is fixed in the prone position. On the hinder side of the

wrist is a small membrane bone, the pisiform. A membrane bone, the knee-cap or patella, covers the knee joint and is connected by ligament with the tibia. The tibia and fibula are fused at their lower ends. The first row of tarsals contains two prominent bones, the astragalus or talus, and the fibulare or calcaneum, which lies outside the astragalus and projects backwards to form the heel.

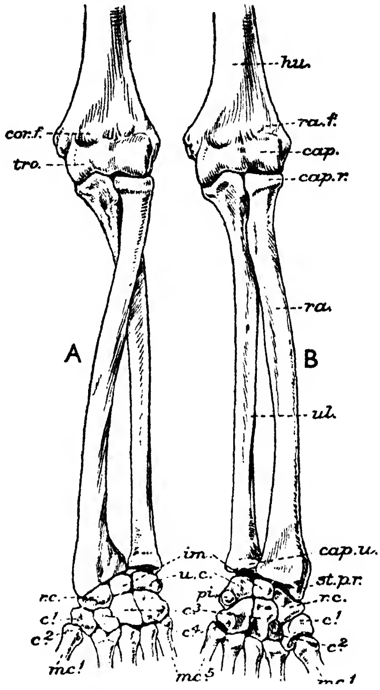


FIG. 24.20.—Bones of the left fore-limb of man.

A, In pronation; *B*, in supination.

c.[1], Os multangulare majus or trapezium; *c.*[2], multangulare minus or trapezoid; *c.*[3], capitatum or magnum; *c.*[4], hamatum or unciform; *cap.*, capitulum of the humerus, with which the radius articulates; *cap.r.*, capitulum of the radius; *cap.u.*, capitulum of the ulna; *cor.f.*, coronoid fossa; *hu.*, humerus; *im.*, os lunare or semilunar; *mc.*[1], *mc.*[5], first and fifth metacarpals; *pi.*, pisiform; *r.c.*, os naviculare or scaphoid; *ra.*, radius; *ra.f.*, radial fossa; *st.p.r.*, styloid process of the radius; *tro.*, trochlea; *u.c.*, os triquetrum or cuneiform; *ul.* ulna.

ALIMENTARY SYSTEM: MOUTH, TEETH, AND PHARYNX

The mouth differs from that of the frog in the possession of mobile, muscular lips, and of a palate—an inner roof which separates from the mouth or buccal cavity a narial passage. By this passage the approach from the nostrils to the mouth is prolonged backwards, so that the internal nares open into the pharynx instead of into the fore-part of the mouth (Fig. 24.21). The first part of the inner roof is strengthened by the horizontal processes of the premaxillary, maxillary, and palatine bones (pp. 426–8) and is known as the hard palate; the hinder part is purely fleshy and is known as the soft palate. The narial passage lies above the palate and below the true olfactory chambers. Over the hard palate it is not separated from these by any roof, and the nasal septum between them comes down to divide it into two (p. 423). Over the soft palate it is single, and is separated from the olfactory chambers by a partition, supported

by the horizontal flanges of the vomer, representing the true roof of the mouth. Into this hinder part, the nasopharynx, open the Eustachian tubes which communicate with the middle ear. The tonsils are a pair of pits at the sides of the soft palate near its hinder border. The tongue is an elongate, muscular mass attached along most of its length to the floor of the mouth, but with a

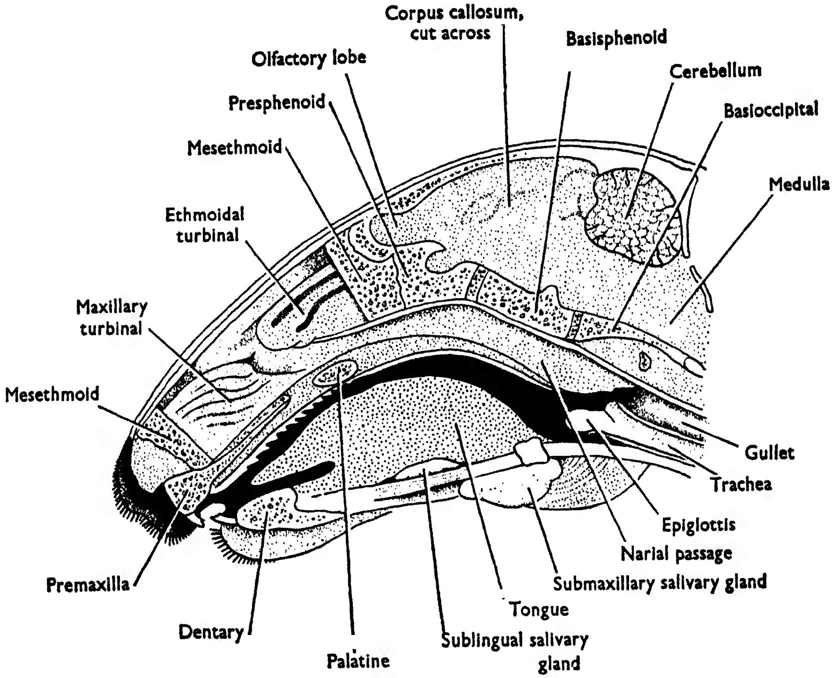


FIG. 24.21.—Rabbit. The head, cut down the mid-line and seen from the left side ; the middle portion of the mesethmoid bone has been removed. × 1.

free tip in front. It bears papillæ of several kinds which are sensitive to dissolved chemical substances and are thus organs of taste.

The teeth have the same basic structure as those of the dogfish and frog and all other vertebrates (Fig. 22.18). The main part is a hollow structure of ivory or dentine, which is roughly bone without blood vessels, divided into the root which is below the surface and the crown which is above. The latter is covered with a very hard material called enamel, and the hollow is filled with soft dental pulp, consisting of connective tissue, blood vessels and nerves. Surrounding the root, and sometimes, especially in

herbivores (Figs. 25.12, 25.13) extending partially over the enamel, is a softer bone-like material called cement. The tooth is anchored to the jaw by the periodontal membrane. Instead of continual replacement throughout life, mammals have two definite sets of teeth, the milk teeth in the young animal and the permanent teeth in the adult. Such an arrangement is called diphyodonty. The nomenclature of heterodont teeth is based, as we have seen, on the bones which bear them, but in most mammals each group has a characteristic shape and function. The incisors are biting teeth, and in the rabbit are chisel-shaped ; the canines are typically large stabbing teeth, but the rabbit has none. The cheek teeth are used for crushing and grinding, and have various patterns in different groups of mammals ; in the rabbit they are all alike, with broad, transversely ridged crowns. In some mammals the anterior cheek teeth, which have milk predecessors and are called premolars, are recognisably different from the posterior ones, called molars, of which only one set occurs in the life of an individual. The distinction of premolars and molars can only be made in the rabbit by an investigation of their development. The numbers of the teeth of a mammal are usually expressed by a formula, which appears as a fraction, incisors, canines, premolars and molars of one side of the upper jaw in the top line, and incisors, canines, premolars and molars of one side of the lower jaw below. The dental formula of the rabbit is $\frac{2033}{1023}$, so that there are twenty-eight teeth in all. Between the incisors and the premolars is a long gap, the diastema. The dental formula for the dog is $\frac{3142}{3143}$, and the fourth upper premolar and first lower molar, which bite against each other, are specially enlarged as shearing teeth or carnassials. The teeth of the rabbit and other herbivores grow throughout life, but in most mammals the roots close and growth ceases when the tooth is fully formed.

Posteriorly the buccal cavity and the narial passage lead into a short pharynx. Behind, this leads above (dorsally) into the gullet and below to the glottis, which lies shortly behind the tongue, covered by a flap, known as the epiglottis, which is stiffened by a cartilage. Thus in the pharynx there cross one another the passages by which the food passes to the alimentary canal and the air to the lungs. When the animal swallows the soft palate is raised and thus closes the posterior nares, while muscles contract

and close the opening of the windpipe, so that when the food is thrust backwards by the muscles of the tongue and pharynx it passes only into the œsophagus or gullet, a tube which runs backwards through the neck and chest, above the trachea. The epiglottis perhaps enables the animal to breathe while eating.

STOMACH AND INTESTINE

Shortly after passing through the diaphragm, the œsophagus joins the stomach (Figs. 24.22, 24.24). This is a broad curved sac, with a wider left or cardiac end and a narrower right or pyloric end. The gullet opens into the middle of the concave anterior surface, and the dark-red spleen lies close against the convex surface. The pyloric end communicates with the intestine by a small opening, the pylorus, provided with a sphincter. The small intestine is a narrow, much-coiled tube, seven or eight feet in length. Its first section or duodenum runs from the pylorus along the right side of the abdomen nearly to the hinder end of the latter and then turns forward, forming a loop. In the mesentery between the two limbs of the loop lies the thin, diffuse pancreas, whose duct enters the returning limb of the loop about three inches behind the bend ; close to this point the rectum is attached to the duodenum by mesentery. The liver is a large, dark-red, lobed organ slung from the diaphragm by the falciform ligament ; in a groove upon its right central lobe lies the elongated, dark-green gall-bladder, from which the bile duct runs backwards to open into the dorsal side of the duodenum shortly beyond the pylorus. The remainder of the small intestine is the ileum ; it ends in a round swelling known as the sacculus rotundus. The lining of the small intestine is beset with numerous minute processes or villi, by which its surface is increased and absorption of food aided. From the sacculus rotundus there opens a very large tube, the blind gut or cæcum, marked by a spiral constriction and ending blindly in a small finger-like vermiform appendix. It starts near the posterior end of the body on the left side, and its main limb runs forward and to the right, then back to the left posterior to the first loop, and finally forward and to the right again in front of the first loop, so that the appendix is on the right side and well in front of the sacculus. A short limb of the cæcum, about an inch long, lies on the other side of

the sacculus. From the sacculus rotundus there also starts the large intestine, in which two regions may be recognised. The colon is a tube, about a foot and half in length, which begins

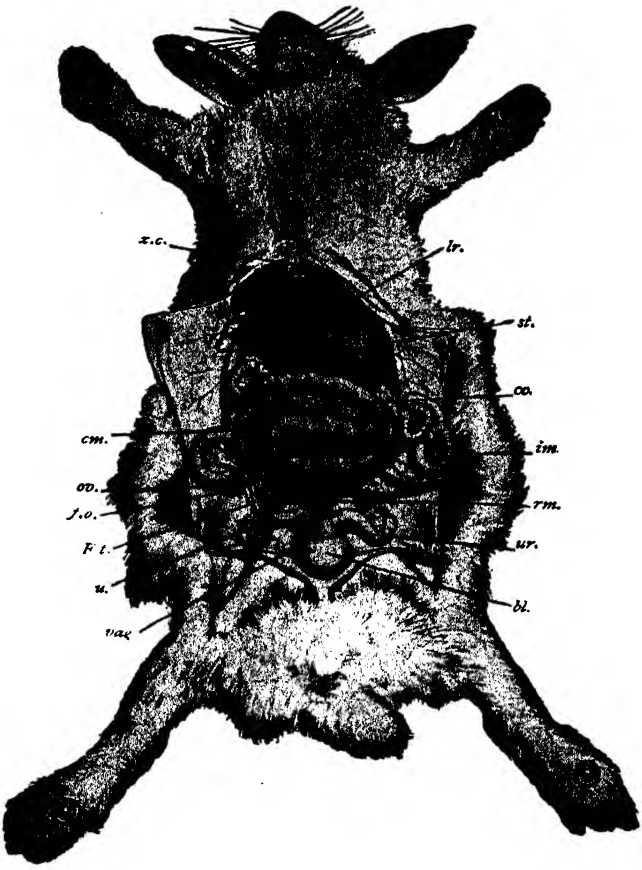


FIG. 24.22.—The body of a female rabbit with the abdomen opened, the organs being somewhat displaced so as to display them. In the natural position the colon and the loops of the cæcum run diagonally across the body from the animal's right to left.

bl., Bladder ; *cm.*, cæcum ; *co.*, colon ; *F.t.*, Fallopian tube ; *f.o.*, fimbriated opening of the oviduct ; *im.*, ileum ; *lr.*, liver ; *ov.*, ovary ; *rm.*, rectum ; *st.*, stomach ; *ur.*, ureter ; *u.*, right uterus ; *vag.*, vagina ; *x.c.*, xiphoid cartilage. Note also : regions of body (head, neck, chest, abdomen, tail), mouth, nostrils, hare lip, prominent incisor teeth, vibrissæ.

by running forward and to the right between the first and third loops of the cæcum ; it is sacculated, or constricted by a number of rings ; the rectum is a narrower tube about two and a half feet long, in which fæcal pellets can be seen.

DIGESTION

The function of the alimentary canal is to digest and absorb the food (p. 7). It is partly broken down mechanically by the

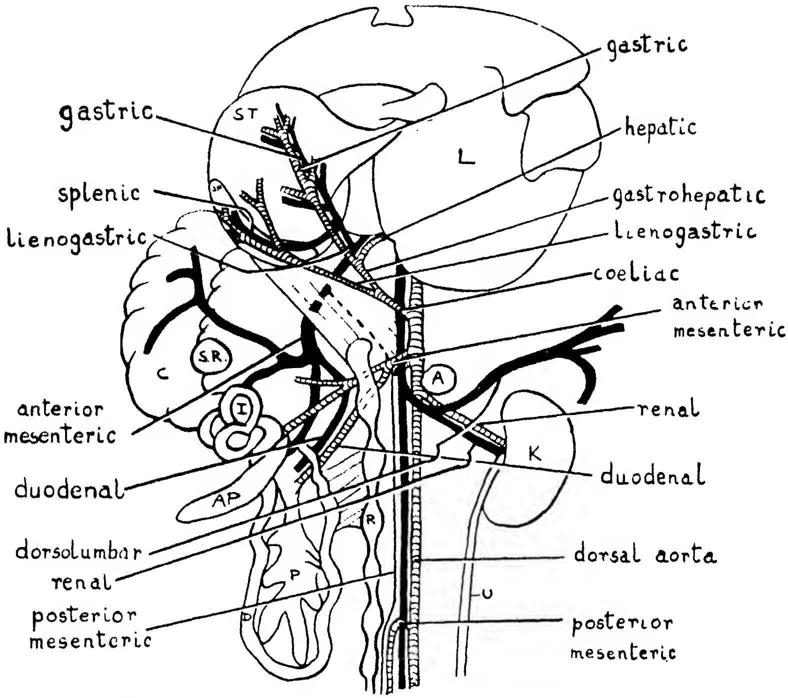


Fig. 24.23.—Rabbit, blood supply of the gut, ventral view, somewhat diagrammatic. The stomach and most of the intestine have been displaced to the animal's right; the ileum and the colon are shown conventionally. Arteries are shown lined, with their names on the right of the diagram, veins in solid black with their names on the left.

A, Adrenal; *AP*, appendix; *C*, colon; *D*, duodenum; *I*, ileum; *K*, kidney; *L*, liver; *P*, pancreas; *R*, rectum; *SP*, spleen; *S.R.*, sacculus rotundus; *ST*, stomach; *U*, ureter.

teeth, but the main attack is chemical. The walls of the stomach and small intestine, and certain special glands, produce enzymes, which hydrolyse the various classes of foodstuff. Carbohydrates are first acted on in the mouth by an amylase (from *amylum* = starch), formerly called ptyalin, in the saliva or spittle. This is secreted by four pairs of salivary glands; the parotids, behind the angles of the jaws, the submaxillaries between the angles, the infraorbitals below the eyes, and the sublinguals inside the

dentaries. Amylase converts starch and glycogen to maltose, a disaccharide.[1] In the small intestine another amylase, produced by the pancreas, continues the breakdown of starch and glycogen, and a series of disaccharases secreted by the intestinal wall break down cane, malt and milk sugars to their appropriate hexoses. The digestion of protein begins in the stomach, where pepsin hydrolyses it to proteoses and peptones. The walls of the

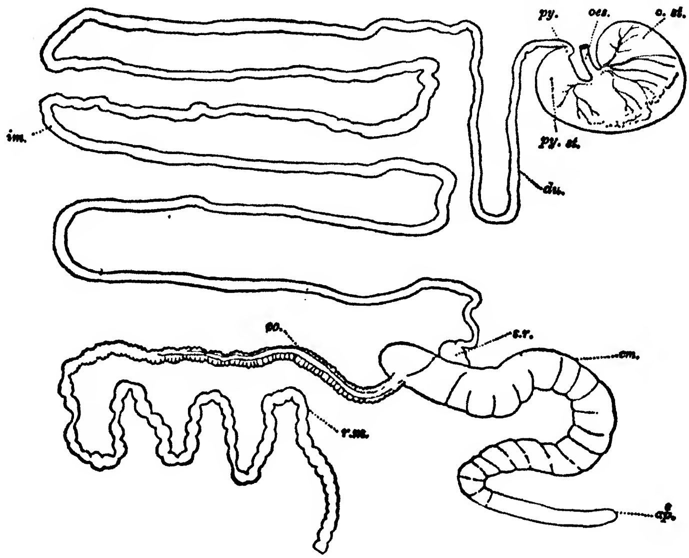


FIG. 24.24.—The alimentary canal of a rabbit removed from the body and spread out.

ap., Vermiform appendix; *c. st.*, cardiac end of stomach; *cm.*, cæcum; *co.*, colon; *du.*, duodenum; *im.*, ileum; *oes.*, œsophagus; *py.*, pylorus; *py.st.*, pyloric end of stomach; *rm.*, rectum; *s.r.*, sacculus rotundus.

stomach also secrete much hydrochloric acid, giving in man a pH of 1. Pepsin can act only in a strongly acid medium, and the acid is also necessary to produce the active pepsin from the inactive pepsinogen that is secreted by the walls of the stomach. In the intestine the protein meets more enzymes, both from the pancreas and the intestinal juice, which together break down proteins through smaller molecules called proteoses, peptones, polypeptides and dipeptides to amino acids. Some details of their

[1] The saliva of the rabbit contains only a low concentration of amylase. So far as is known, high concentrations are present only in primates and elephants, and many mammals, especially the carnivores, have little or none.

action are shown in Table VI. The intestinal contents are approximately neutral in reaction. Fat is broken up physically into very fine droplets by the bile, and partially hydrolysed to glycerol and free fatty acid by lipases from the stomach, pancreas, and small intestine. The digestion is partly under nervous, and partly under hormonal control (p. 469).

Absorption of the digested food takes place in the small intestine. Hexoses, amino acids, and some fatty acids go into the blood capillaries and so by the portal vein to the liver ; most of the fatty acids, glycerol and possibly some unsplit fats go into the cells of the villi ; in there fat is resynthesised and passed into the lymphatic vessels, from which it goes to the general circulation (p. 451) and the fat depots of the body. Water is largely absorbed in the colon.

The enzyme system of vertebrates is not capable of breaking down the cellulose cell walls of plants, which make a great part of the food of the rabbit. In the cæcum, where the food stays for some time, they are attacked by bacteria, which may be regarded as symbionts. They change the cellulose into a form which the rabbit could use, but it is below the point where digestion and absorption are possible ; there has therefore been developed a peculiar type of feeding called reingestion or refection, or pseudorumination. Freshly eaten food passes very quickly through the stomach and small intestine to the cæcum. Early next morning it is passed out as soft fæces without drying, and these are at once eaten by the rabbit. They pass to the cardiac stomach and remain there while fresh food passes straight through as before. The fæces-food is digested in the ordinary way in the stomach and intestine ; it does not re-enter the cæcum, but passes slowly through the large intestine so that water is absorbed and the normal dry fæcal pellets are produced. Refection is specially important in giving an adequate supply of protein, and perhaps of vitamin B. It increases in cold weather. It is found in other animals, including the hare, many rodents and the common shrew.

TABLE VI

PROTEOLYTIC ENZYMES OF THE SMALL INTESTINE OF MAMMALS

Place of secretion	Enzyme	Activation	pH optimum	Substrate	Point of application	Products
Pancreas	Trypsin	Trypsinogen unmasked by enterokinase, or by trypsin already present	8–11	Proteins Proteoses Peptones	Peptide links at ends of chain and in middle, formed from carboxyl group of lysine or arginine	Polypeptides, and amino acids, especially lysine and arginine
"	Chymotrypsin	Chymotrypsinogen unmasked by trypsin	7.5–8.5	Proteins Proteoses Peptones	Peptide links at ends of chain and in middle, formed from carboxyl group of an aromatic acid	Polypeptides, and amino acids, especially tyrosine and phenylalanine
"	Carboxypeptidase (probably many)	Procarboxypeptidase unmasked by trypsin	c. 7.3	Polypeptides	Terminal peptide link adjacent to free carboxyl group	Dipeptides and amino acids
"	Elastase	Proelastase unmasked by trypsin	8–9	Most proteins except keratin and collagen, but especially elastin		Soluble proteins
Small intestine	Aminopeptidase (probably many)	By metallic ions	8.0	Polypeptides	Terminal peptide link adjacent to free amino-group	Dipeptides and amino acids
"	Dipeptidases (probably many and specific)	By metallic ions	7.5–8.0	Dipeptides, e.g. glycylglycine	Amino—and carboxyl groups, and peptide link	Amino acids

From Yapp, *An Introduction to Animal Physiology*, 2nd edition, 1960. Clarendon Press, Oxford.

RESPIRATORY ORGANS

The glottis (p. 437) leads into a short larynx and this into a longer trachea, or windpipe. Both trachea and larynx are supported by cartilages, which partly represent the branchial arches (p. 316). The cricoid cartilage is a complete ring, but the thyroid and the tracheal rings are incomplete dorsally. The larynx contains the vocal cords, small bands of muscle attached to the arytenoid cartilages. Their vibration, the quality of which is altered by variation in their tension, is caused by air moving past them, and produces the voice. The rabbit is remarkably silent. The trachea passes into the thorax, and there divides into two bronchi. Each of these divides and subdivides into fine bronchioles, and the mass of these makes the lung. The end of each terminal bronchiole is expanded into a blind air sac or infundibulum, and the walls of this are hollowed out into air cells or alveoli. These are supplied with fine blood vessels, and the whole lung is thus not a hollow sac like that of the frog, but a spongy mass with a greatly increased internal surface ; in man this is about thirty times the surface area of the body.

The chest or thorax is a closed box whose side walls are formed by the ribs with the muscles between them, and its hinder wall by the diaphragm, which divides the main or pleuroperitoneal cœlom, parting two pleural cavities in front from a peritoneal cavity behind (p. 417). The cavity of the thorax can be enlarged from back to breast, by a contraction of the intercostal muscles which move the ribs outwards (and in man upwards) ; and from head to tail by the movement of the diaphragm, which at rest is convex towards the chest, but flattens when it contracts, thus increasing the size of the thorax. Since the pleural cavities are closed, their enlargement lowers the pressure within them, and thus the lungs, which are elastic and contain air at atmospheric pressure, must expand also to equalise the pressure on the two sides of their walls. The air in them thus in turn has its pressure lowered, and since they are open to the atmosphere, air moves in from outside to maintain equilibrium. When the inspiratory muscles relax, air is driven out by the collapse of the chest owing to the elasticity of the lungs, but this can be aided by the contraction of certain other muscles, notably those of the belly, which press the viscera against the diaphragm from behind. After air has been taken into the lungs, oxygen which has

diffused from the alveoli into the capillaries combines with the hæmoglobin of the red cells and is carried to the tissues (For respiratory regulation, see p. 15.)

BLOOD VESSELS: HEART

The blood of the rabbit, like that of all vertebrates, is contained in a closed system of vessels. The heart is the pumping organ, vessels which take blood away from it are arteries, and those

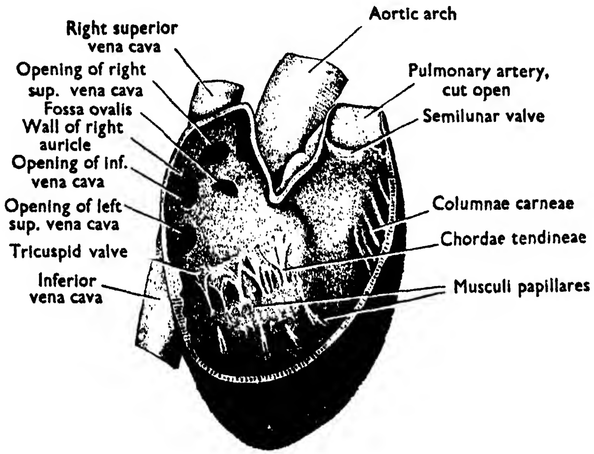


FIG. 24.25.—The heart of a rabbit from the right side, with the outer wall of the right auricle and the right ventricle removed. × 1.

which bring blood back to the heart are veins. Arteries break up into smaller vessels called arterioles, and these in turn into very fine capillaries, which form a network in nearly every organ. Capillaries join together to give venules, and these in turn unite to form veins. A vein which drains blood from one set of capillaries and takes it to another set is, together with this second set, called a portal system.

Arteries in general have relatively thick muscular walls, while those of veins are thinner and more elastic, and the blood shows through them in dissection. Veins often contain watch-pocket valves to prevent the reverse flow of blood (Fig. 27.37).

The heart of the rabbit lies in the front part of the chest, enclosed in the thin pericardium immediately behind the soft, pink thymus. It has four chambers, two auricles and two ventricles. Three venæ cavæ corresponding to those of the frog open directly

into the right auricle (Fig. 24.25), and two pulmonary veins lead by a common opening into the left auricle. The opening from the right auricle into the right ventricle is guarded by a threefold tricuspid valve fastened to the ventricular wall by chordæ tendineæ, and a similar twofold mitral valve guards the opening between the chambers of the left side. The two sides do not communicate with one another, but the site of an opening between the two which is present in the embryo is marked by the fossa ovalis. From the front end of the right ventricle arises the pulmonary artery, and from the front of the left ventricle, above the pulmonary artery, arises the single aortic arch. The opening of each of these vessels is provided with three semilunar valves. The pulmonary artery divides to supply the two lungs, and the arteries to the head and arms arise from the arch of the aorta, which afterwards supplies the trunk. In the beating of the heart, the auricles contract simultaneously, and the ventricles follow immediately afterwards ; then after a short pause the auricles start another contraction. The venous blood which reaches the right auricle from the capillaries of the body is driven by the auricular contraction into the right ventricle and thence in turn through the pulmonary artery to the lungs. Returning oxygenated to the left auricle it is driven into the left ventricle, and thence through the aorta to all parts of the body. There is thus a double circulation, as in the frog, but the separation of the ventricles and connection of the pulmonary artery with one of them and the aorta with the other ensures that there is no mixing of oxygenated and deoxygenated blood.

REGULATION OF THE CIRCULATION

The supply of blood which an organ receives depends on two factors : (1) the width of the small blood vessels in the organ, (2) the pressure under which the blood is flowing. When an organ such as a muscle is active, its small vessels are caused to dilate by the presence of carbonic acid (p. 15) and other products of the activity of its tissues, and also by the action of the nervous system. Now any dilatation of blood vessels, by enlarging the bed of the blood stream, tends to lower the general blood pressure, and thus both to diminish the local effect of enlarging the vessels, and also to have injurious results in other organs. These tendencies, however, if they be on a sufficient scale, are counteracted through

the nervous system in two ways—by an acceleration of the rate of the heartbeat, and by the contraction of vessels in other parts of the body (in this case, of the alimentary canal and of the spleen), so that the total capacity of the vascular system is not increased.

ARTERIES

The aortic arch (Fig. 24.26) bends over to the left and, as the dorsal aorta, passes backwards under the backbone through the chest and abdomen till it becomes the small caudal artery. A ligamentous band, known as the ductus arteriosus, connects the aortic arch with the pulmonary artery, just before the bifurcation of the latter. At one stage in development this band is represented by an open tube (p. 609). In its course the aorta gives off numerous arteries, of which the following are the most important : (1) a pair of common carotids, each passing up the neck and forking opposite the angle of the jaw into external and internal branches, (2) a pair of subclavians arising from the aortic arch, and going to the shoulder and fore limbs, (3) the cœliac, which arises from the dorsal aorta shortly behind the diaphragm and divides into the hepatic and the lienogastric, (4) the anterior mesenteric, shortly behind the cœliac, (5) the renal arteries, (6) the genital arteries, (7) the small posterior mesenteric, (8) the common iliac arteries ; these last arise just before the hip girdle and practically end the dorsal aorta, which after them is diminished to the caudal artery. Each common iliac gives off an iliolumbar to the body-wall, a vesical to the bladder, and divides into internal and external iliacs. There is considerable variation in the layout of the origins of carotids and subclavians, the commonest variant being the possession of an innominate, from which the right carotid and right subclavian branch off. Two small coronary arteries from the base of the aorta supply the heart muscle.

VEINS

Each superior vena cava (Fig. 24.27) is formed by the union of a subclavian vein from the shoulder and fore-limb, an external jugular from the surface of the head, and an internal jugular from the brain. The external jugulars are connected by an anastomosis across the ventral surface of the neck. The right superior vena cava receives also an azygos vein from the walls of the chest.

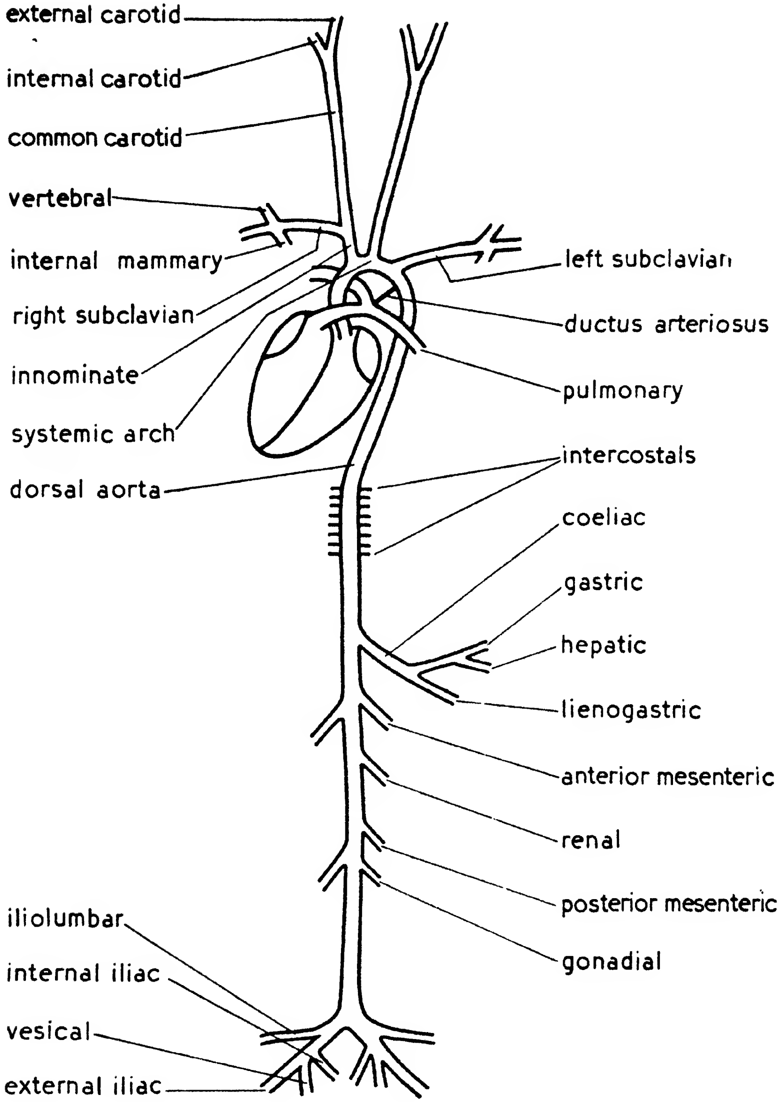


FIG. 24.26.—A diagram of the arterial system of a rabbit.

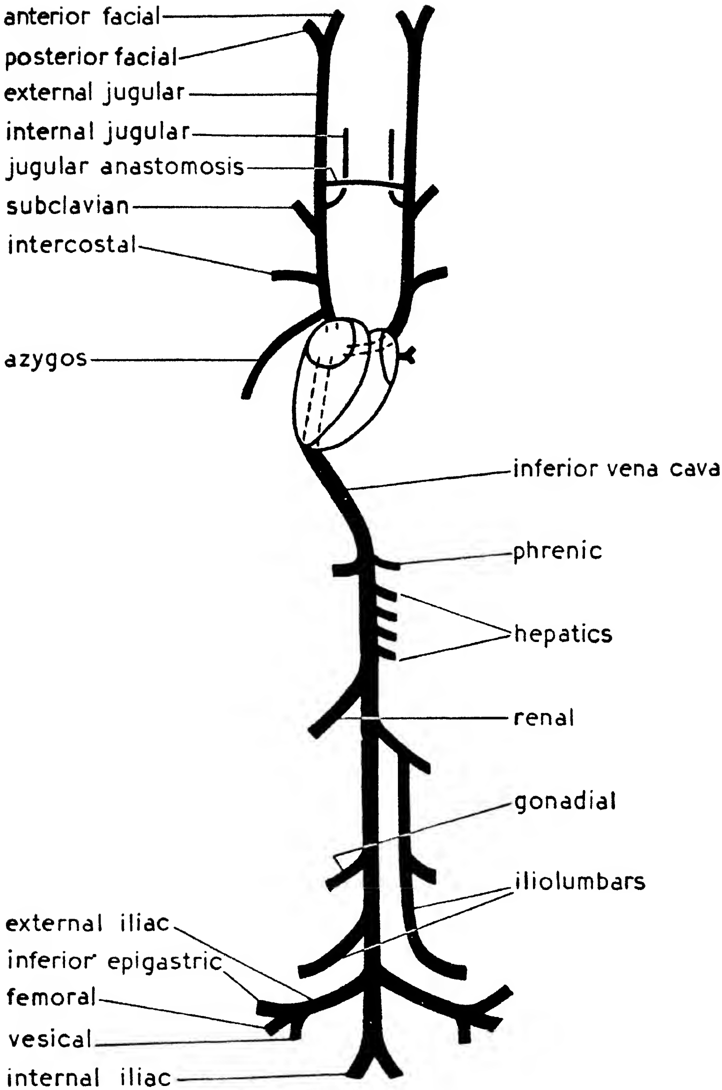


FIG. 24.27.—A diagram of the venous system of a rabbit.

The external jugular is larger than the internal and lies nearer the surface in the neck. The inferior vena cava is a large median vessel which lies beside the dorsal aorta. It receives the following veins (1) the internal iliacs or hypogastrics from the back of the thighs, (2) the external iliacs from the inside of the thighs, (3) the iliolumbars from the hinder part of the abdominal walls, (4) the genital veins, (5) the renal veins, (6) the large

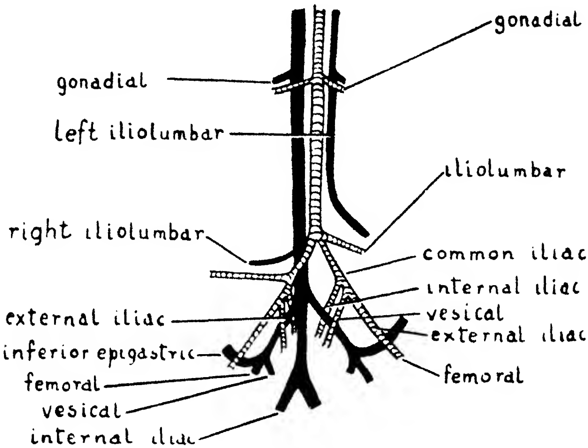


FIG. 24.28.—Drawing of a dissection of the main arteries and veins of the pelvic region of a rabbit. The arteries are shown lined with their names on the right of the figure, the veins in solid black with their names on the left.

hepatic veins from the liver, through which organ it passes on its way to the heart. Instead of going directly to the inferior vena cava, the left genital may join the iliolumbar or the renal, and the iliolumbar may join the renal. Blood from the stomach, intestines, pancreas, and spleen is carried to the liver by the portal vein, but there is no renal portal system (p. 329). In many mammals, such as the rat and cat, but not the rabbit, much of the oxygen supply of the liver comes from the portal vein. This happens because when the stomach is under sympathetic stimulation (p. 622) the arteriovenous channels in its walls are dilated and there is little fall in the oxygen concentration as the blood flows through them.

BLOOD

The blood is a fluid, with proteins, glucose, salts, and other substances in solution, and two main types of cell. The first of

these, the red cells, are biconcave discs without nuclei, which contain hæmoglobin, and the others, the white corpuscles, are of various types, but all contain at least one nucleus. Details of

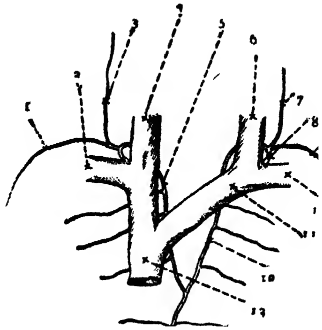
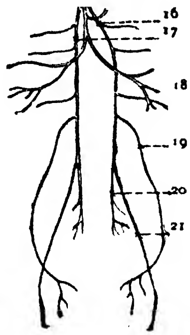


FIG. 24.29.—Main lymph vessels, and branches of the superior vena cava of man (diagrammatic).

1, Right subclavian lymph-trunk; 2, right subclavian vein; 3, right jugular lymph-trunk; 4, right internal jugular vein; 5, broncho-mediastinal (lymph) duct; 6, left internal jugular vein; 7, left jugular lymph-trunk; 8, thoracic duct; 9, left subclavian lymph-trunk; 10, left subclavian vein; 11, left innominate vein; 12, thoracic duct; 13, superior vena cava; 14, thoracic duct; 15, cisterna chyli; 16, left lumbar lymph-trunk; 17, right lumbar lymph-trunk; 18, intestinal lymph-vessels; 19, testicular lymph-vessels; 20, lymph-vessels from pelvis; 21, lymph-vessels from leg.



these cells, and of the other constituents of the blood, will be found on page 528. The pressure in the blood, caused by the heartbeat, forces water and crystalloid solutes out of the capillaries, where they are joined by white cells which force their way through cracks between the cells of the walls. The resulting

blood minus red cells and proteins is called lymph, and it is this which carries food and oxygen to the living cells of the body. Some of the lymph is sucked back into the venous capillaries by osmosis, because the blood pressure is here lower than the osmotic pressure of the proteins in the blood, but most of it is collected into lymphatic vessels. Those from most of the body join together and open into the left subclavian vein at its junction with the external jugular, but those of the right side of the head and neck and right fore-limb open into the right subclavian at the corresponding point. The lymphatic system of man, which is substantially similar to that of the rabbit, is shown in Fig. 24.29.

It is obvious from its almost universal occurrence in the higher animals that blood must be important in their life. A fuller account of its many functions, which are seen at their greatest number in mammals, is given on page 189, and some details of its physiology will be found elsewhere in this book. It is primarily a means of transport, and the things which it carries are five : oxygen in the red cells (p. 528) ; food in solution (p. 442) ; excretory products including carbon dioxide in solution, and carbon dioxide in the red cells (p. 529) ; hormones (p. 469) ; and heat. Secondly, the blood, in conjunction with other organs, regulates its own composition, so as to provide a constant internal environment for the cells of the body (p. 189). Thirdly, it is used for a number of miscellaneous minor purposes ; in some mammals, such as man and notably many monkeys, it imparts colour to the body, and it is used mechanically for the erection of the penis.

In mammals and birds the blood vascular system is also important in temperature regulation. In these warm-blooded or homoiothermic animals the temperature of the body is kept constant within very narrow limits, whatever the temperature of the surroundings. The usual temperature of mammals is about 38° C. Control is obtained in two ways : as the temperature outside falls, the amount of heat produced by the resting muscles increases, so that more is available to be lost to the environment, and at the same time the surface capillaries of the body contract so that less blood flows through the skin and less heat is brought to the surface to be lost. The result is that the temperature of the skin falls but not that of the rest of the body. The reverse processes occur when the temperature rises. In some mammals, notably man, the sweat glands are also important, particularly at high temperatures, when they produce much water which

takes much heat from the body by evaporation. In others, such as the dog, panting helps to prevent the body temperature from rising. A rapid intake of air into the mouth but not the lungs causes increased evaporation from its moist surface.

EXCRETORY ORGANS

The kidneys of the rabbit are a pair of dark-red bodies, convex on the outer side and concave on the inner, which lie on the dorsal wall of the peritoneal cavity, that on the left side farther back than that on the right. Like those of the dogfish and frog they consist of tubules, but these even in the embryo do not open into the peritoneal cavity. Each begins as a Bowman's capsule (Fig. 22.34), which contains a small part of the cœlom, and has pushed into one side of it the glomerulus, a cluster of blood vessels supplied from the renal artery. Capsule and glomerulus are known as the Malpighian body. From the capsule there leads away the tubule. The tubules join together into collecting ducts, and finally open into the ureter, a duct which has no counterpart in dogfish or frog. From the concavity or hilus of the kidney the ureter runs back to open into the bladder. In the early stages of development this organ joins the rectum in a cloaca, but later the latter becomes divided, so that excretory and fæcal products are not mixed. The opening of the bladder is different in the two sexes and is described below.

Fluid withdrawn from the cavity of the capsule is found to be identical with the plasma of the blood except that it contains no colloids. The wall of the glomerulus together with that of the capsule has acted as a dialyser, and since the osmotic pressure of the colloids is less than the hydrostatic pressure in the renal artery, water and crystalloids are forced out of the capillaries into the capsule. The distinction is not in fact strictly between crystalloids and colloids, for experiments show that proteins with a lower molecular weight than about 70,000 are passed out. Since hæmoglobin has a molecular weight of 67,000 the advantage of its being enclosed in capsules is obvious.

As the filtrate from the glomerulus passes down the tubule two things happen to it. Ninety to 99 per cent. of the water, nearly all the glucose, chloride and amino acids and smaller proportions of other solutes are absorbed, chiefly in the proximal tubule and loop of Henle, and at the same time some solutes, especially

phosphate, sulphate, urea and ammonia, are excreted by the tubule. The result, the urine, is much more concentrated than the glomerular filtrate, and contains relatively more of the excretory products.

The control of the kidney, by the autonomic nervous system and hormones from the posterior pituitary, the adrenal cortex and the parathyroid, is very complicated, and the final result is that however much water is absorbed from the intestine or lost in sweat, the composition of the blood is kept constant within very fine limits.

REPRODUCTION

The testes (Fig. 24.30) are a pair of ovoid bodies which arise in the course of development on the dorsal wall of the peritoneal cavity near the kidney, but later become free and pass backward through the inguinal canals into two pouches of the body-wall at the sides of the penis known as the scrotal sacs. Each testis remains connected with its original position by a spermatic cord, which consists of connective tissue with an artery, vein, and nerve. In passing backwards it carries with it a part of the kidney corresponding to that which is functional in the frog, which in the adult may be seen as the epididymis, lying along the side of the testis and enlarged at the front and hind ends into a caput and cauda respectively. The cauda epididymis is connected to the scrotal sac by a short, elastic cord known as the gubernaculum. Each epididymis consists of a mass of twisted tubules joining into a single, much-coiled tube which becomes continuous at the cauda with the vas deferens (or ductus deferens). This passes forwards out of the scrotal sac, curves over the ureter, and passes backwards again to open with the mouth of a small median sac known as the uterus masculinus, which lies above the neck of the bladder within the pelvic girdle ; it is absent from some rabbits, but is large in many mammals, for example the guinea-pig. The uterus masculinus opens into the neck of the bladder, which is known after their junction as the urinogenital canal or urethra, and passes backwards into the penis, at the end of which it opens. Beside the uterus masculinus lie the prostate glands which pass their secretion into the urethra, and behind the prostate are Cowper's glands. The products of the testes and all these glands make the semen. The penis is situated behind the symphysis

pubis and in front of the anus. It has spongy, vascular walls and is invested by a loose sheath of skin, the foreskin or prepuce, which hangs forwards over the tip or gland of the organ. In sexual excitement the penis is stiffened or erected by the flow of blood

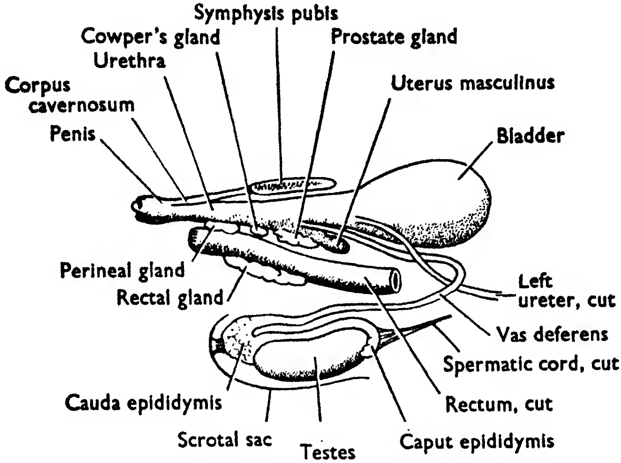


FIG. 24.30.—Rabbit. The male reproductive organs, from the left side, ventral surface uppermost. × 1.

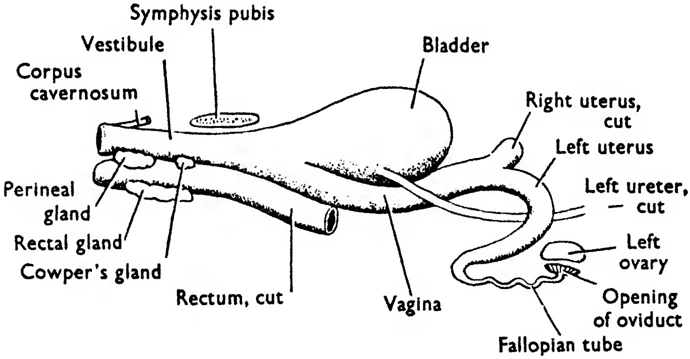


FIG. 24.31.—Rabbit. The female reproductive organs, from the left side, ventral surface uppermost. × 1.

into venous spaces which it contains, and in this state is thrust rhythmically in and out in the vagina of the female. This causes a reflex contraction of muscles of the vasa deferentia, which ejaculates the semen containing the sperm into the female. The whole act is known as coition or copulation.

The ovaries (Fig. 24.31) are small, oval bodies attached behind the kidneys to the dorsal abdominal wall, and show on their surface little blister-like projections, known as Graafian follicles, each of which contains a microscopic ovum. The oviducts open into the abdominal cavity by wide, funnel-shaped fimbriated openings just outside the ovaries. When the ova are ripe the follicles burst and discharge the ova into the funnels, which at that time extend over them. The first section of each duct is narrow and gently sinuous and is known as the Fallopian tube. It runs backwards and enlarges into the uterus, a vascular-walled structure which joins its fellow in the middle line anteriorly to the bladder to form the vagina. This passes backwards within the pelvic girdle above the neck of the bladder, with which it presently unites to form a short urogenital canal or vestibule, which opens at the vulva. On its ventral wall lies the small, rod-like clitoris and on the dorsal wall two small Cowper's glands.

The female mammal will normally receive the male only at certain periods, when she is said to be in œstrus or on heat, and in some mammals, such as the sheep, the ripening of ova and their discharge, or ovulation, takes place automatically at these times; the rabbit will copulate at any time, and ova are not discharged except after coition. The spermatozoa travel up the oviducts and fertilisation takes place at the upper ends of the latter. The ova then pass down the oviducts, in which they segment. At the end of the third day they reach the uterus. Here at first they lie free. On the eighth day, however, they begin to become attached to the uterine wall, and in the course of the next few days there is formed in connection with each of them a special organ, known as the placenta, in which blood vessels derived from the mother and the developing young are in very close and extensive contact. Through the thin walls of the two sets of blood vessels interchange of fluid and gaseous contents takes place, and in this way the nutrition and respiration of the young are provided for until birth, which takes place at the end of a month from fertilisation. Animals in which, as in the rabbit, a great part of development takes place within the body of the mother, so that the young when they are born are beyond the need of a shell or similar covering, are said to be viviparous. The wild rabbit may breed in any month of the year, but the main season is from January to June, when almost all females become pregnant at every œstrus, so that there may

be about eight litters a year. More than half of the litters are never born, but are completely resorbed into the uterus; this happens more often with the larger litters, so that the most productive litter size is the average of five to six. The animals are polygynous rather than promiscuous, the dominant buck of a group serving all the does, and other bucks only a few. They are able to breed at six months. Before producing her young the female makes a nest of leaves, and fur from her own body. The life of a rabbit may be seven or eight years.

NERVOUS SYSTEM

The actions of the body are for the most part co-ordinated by the nervous system. In the vertebrate this has two main parts—the cerebrospinal system, connected with the organs of sense and the voluntary muscles; and the autonomic system, connected principally with the viscera and blood vessels. The cerebrospinal system comprises the central nervous system or cerebrospinal axis, composed of the brain and the spinal cord, and the peripheral nervous system, containing the cerebrospinal nerves and certain knots of nerve cells upon them, known as their ganglia. The cerebrospinal nerves are usually twelve pairs of cranial nerves arising from the brain, and a variable number of spinal autonomic nerves. The system also consists of nerves and ganglia. Nerves are made up of nerve fibres, and these are either afferent, conveying impulses from sense organs to the central nervous system, or efferent, taking impulses out to muscles and glands and other effector organs which do the work of the body. The central nervous system has an inner grey matter, consisting chiefly of nerve cells, and an outer white matter, mainly of nerve fibres which run up and down the spine. The detailed structure of fibres and cells is shown on pages 514–16.

The spinal cord runs the whole length of the neck and body, within the neural canal of the vertebrae; at its front end it is continuous with the brain, and posteriorly, a little in front of the sacrum, it narrows to a thin filament, the filum terminale, which continues into the tail. It is more or less cylindrical, but somewhat flattened dorsoventrally and has a small median canal. Its appearance in section is described on page 538.

THE BRAIN

The brain (Figs. 24.32–24.34), which is in origin simply an expansion of the spinal cord, may be divided into fore-, mid-, and hind-brain. The most conspicuous part of the fore-brain is the cerebrum, which consists of two very large cerebral hemispheres divided by a deep cleft or median fissure, at the bottom of which

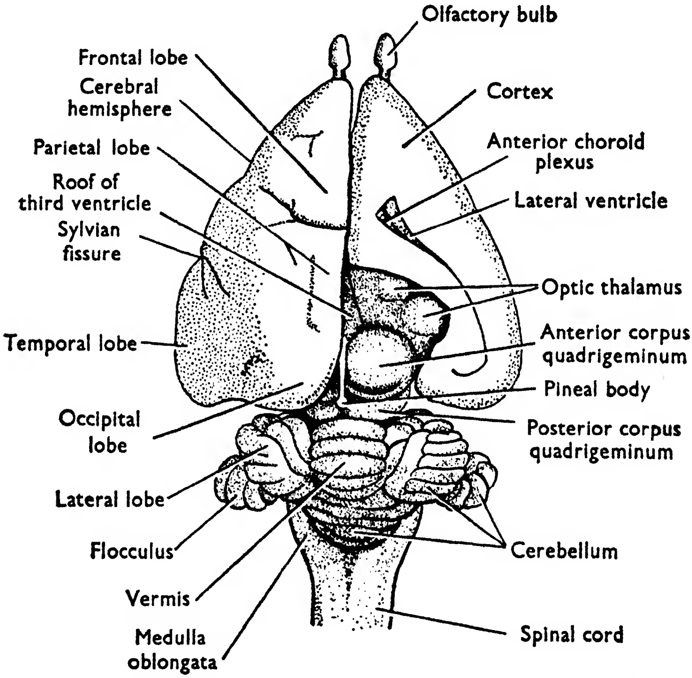


FIG. 24.32.—Rabbit. A dorsal view of the brain, with part of the right cerebral hemisphere cut away. × 1.

they are joined by a bridge known as the corpus callosum, composed of nerve fibres, nearly all of which run transversely. In the cerebrum the grey matter has migrated from around the central cavity to the dorsal surface or pallium, where it forms a cortex. It is almost smooth, but there can be seen on it faint indications of some of the furrows or sulci which in man are deep and numerous and divide the surface into convolutions. Midway at the side of each hemisphere is a shallow groove, known as the lateral or Sylvian fissure, which separates a posterolateral temporal lobe from the frontal and parietal lobes. On the under

side a longitudinal rhinal fissure marks off the frontal and temporal lobes from a region median to them known as the rhinencephalon, which consists of a pyriform lobe behind and the olfactory lobe in front. The latter consists of the olfactory tract and the olfactory bulb, which projects in front beyond the frontal lobe.

In each hemisphere the pallium with its cortex extends over

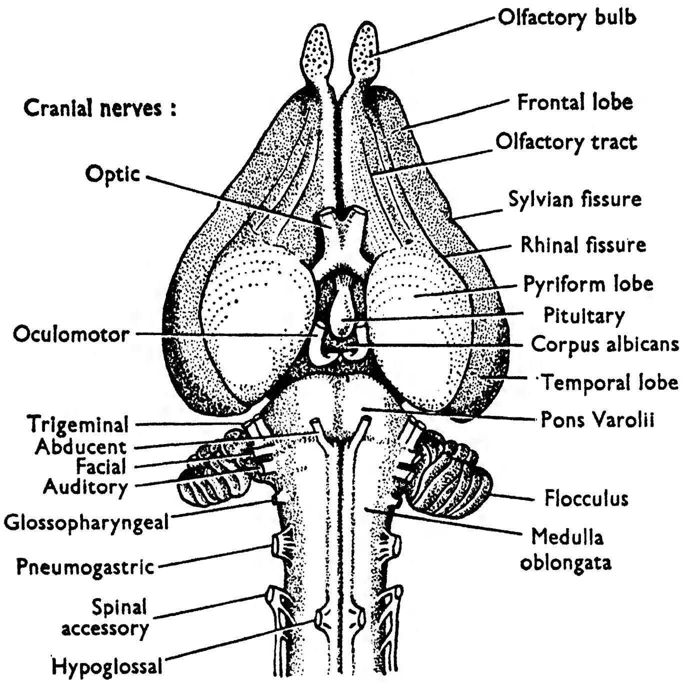


FIG. 24.33.—Rabbit. A ventral view of the brain. × 1.

the corpus striatum, where the grey matter remains internal. This disposition is due to a great expansion of an area (the neopallium) of the dorsal region of the pallium of lower vertebrates, which has thrust apart the lateral and median regions. These now occupy only small areas—the pyriform lobe on the ventro-lateral aspect, and the hippocampus, which has been tucked in on the median side and is now mainly internal. With the development of the neopallium is connected the increased power of co-ordination possessed by the highest vertebrates,

and the great extent of this region in mammals is accompanied by the ability to meet new situations by new behaviour.

The remaining part of the fore-brain, the thalamencephalon, is overhung and hidden by the cerebral hemispheres. Its thick sides form two large thalami, and from the hinder part of its thin roof the pineal stalk passes backwards to end in the pineal body between the hinder ends of the hemispheres. The infundibulum is a funnel-like depression of the floor of the thalamencephalon, which enters the pituitary body. The latter, with the bottom of the infundibulum, is usually torn off in removing the

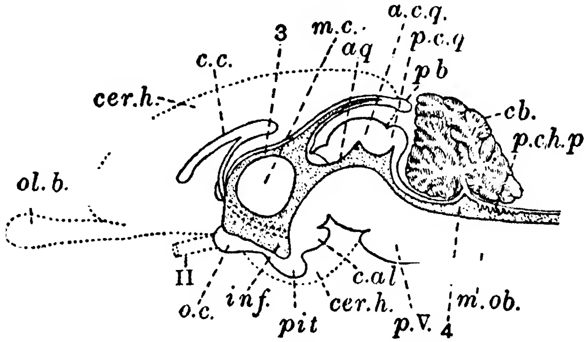


FIG. 24.34.—A semi-diagrammatic, median, longitudinal section of the brain of a rabbit.

a.c.q., Anterior corpus quadrigeminum ; *aq.*, aquæductus Sylvii ; *c.al.*, corpus albicans ; *cb.*, cerebellum ; *c.c.*, corpus callosum ; *cer.h.*, cerebral hemisphere ; *inf.*,infundibulum ; *m.c.*, middle commissure, which connects the two optic thalami across the third ventricle ; *m. ob.*, medulla oblongata ; *o.c.*, optic chiasma ; *ol.b.*, olfactory bulb ; *p.b.*, pineal body ; *p.c.q.*, posterior corpus quadrigeminum ; *p.ch.p.*, posterior choroid plexus ; *p.V.*, pons Varolii ; *pit.*, pituitary body ; II, optic nerve ; 3, 4, ventricles.

brain from the skull, leaving a longitudinal slit which leads into the third ventricle or cavity of the thalamencephalon. A small, rounded, median swelling immediately behind the infundibulum is known as the corpus mammillare or corpus albicans. The midbrain is almost covered by the cerebral hemispheres. Behind each of its optic lobes there is one of auditory function, so that four corpora quadrigemina or colliculi are seen. The floor and walls of the midbrain are prominent crura cerebri. The anterior part of the hind-brain, the cerebellum, is very large and much folded and consists of a median lobe or vermis and two lateral lobes, each of which bears on its outer side a small lobe, known as the flocculus. The lower side of the hind-brain is crossed in front by a wide flat band of transverse fibres, the pons Varolii, which connects the two halves of the cerebellum. Behind the cerebellum the medulla oblongata, with a space, the fourth ventricle, in it,

narrows backwards into the spinal cord. It is marked by a ventral fissure bordered by two longitudinal bands or pyramids.

There is no ventricle in the cerebellum, but small offsets of the aquæductus Sylvii, the cavity of the mid-brain, enter the

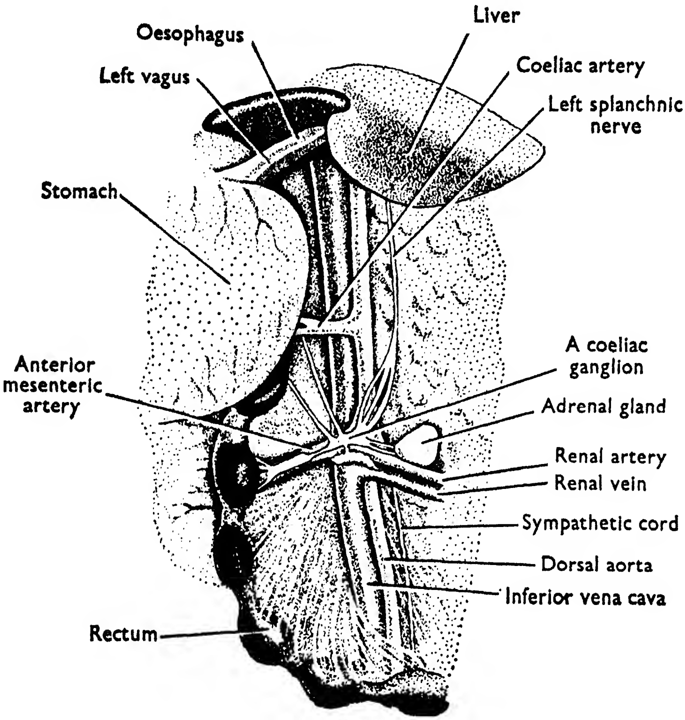


FIG. 24.35.—Rabbit. A dissection of the region of the solar plexus ; the stomach is displaced to the right. × 1.

corpora quadrigemina. The third ventricle in the thalamencephalon is deep, but very narrow, and is crossed by a large middle commissure, which connects the thalami. The lateral ventricles in the hemispheres are wide, shallow, and curved.

CRANIAL AND PERIPHERAL NERVES

The peripheral nervous system is divided into the cranial nerves, which emerge from the brain inside the skull, and the spinal nerves which leave the spinal cord between the vertebræ.

The cranial nerves are twelve pairs. The first ten resemble those

of the dogfish (p. 340) in origin and function, but differ in details: thus the branches of the olfactory nerves leave the olfactory bulb to pass at once through the cribriform plate (p. 423). The optic nerve comes from the thalamencephalon, from which a relay of fibres goes forwards to the cerebral hemispheres. The facial has no ophthalmic branch, and, as in the frog, its buccal branch, all the lateral line nerves, and the pretrematic branches of the glossopharyngeal and vagus, are lost. From the vagus ganglion a pharyngeal goes to the pharynx, an anterior laryngeal forward, and a thin depressor branch to the heart; the main vagus branch runs to various viscera; it gives off also a recurrent laryngeal which loops round the ductus arteriosus on the left side, the subclavian on the right, and runs forward to the larynx. The eleventh or accessory nerve arises from the side of the medulla and spinal cord by a number of roots, the first of which is just behind the vagus and the last at the level of the fifth spinal nerve. It supplies certain muscles of the neck. The twelfth or hypoglossal nerve also arises by several roots which are situated on the ventral side of the medulla, outside the pyramid; it has a branch running forward to the tongue and another running backwards to the larynx. Some of the nerves of the neck are shown in Fig. 24.36.

There are thirty or so pairs of spinal nerves, of origin similar to those of the dogfish (p. 337). The fourth and fifth nerves of the neck give off a branch, the phrenic, which is conspicuous in the dissection of the neck; it runs back through the thorax and supplies the diaphragm. The last three nerves of the neck, together with the first of the thorax, unite to form a network called the brachial plexus; from this several nerves run down the fore-limb. The last four nerves of the lumbar region unite with each other and the two sacral nerves to form a lumbosacral plexus; from this the great sciatic nerve descends the leg, and a number of other branches supply the genital organs and other parts of the abdomen and hip.

Each spinal nerve has near its origin a small ramus communicans to the autonomic or sympathetic system, which is chiefly a chain of ganglia, with connectors, running down in the body below the vertebræ. At the anterior end it communicates with the third, seventh, ninth, and tenth cranial nerves. It gives nerves especially to the viscera, but also to the skin and many other parts of the body, perhaps all. Some of these nerves associate in large ganglia. The most conspicuous of these is the group

called cœliac around the base of the anterior mesenteric artery, the group and its connections making the solar plexus (Fig. 24.35). The autonomic system is discussed more fully on pages 621–3.

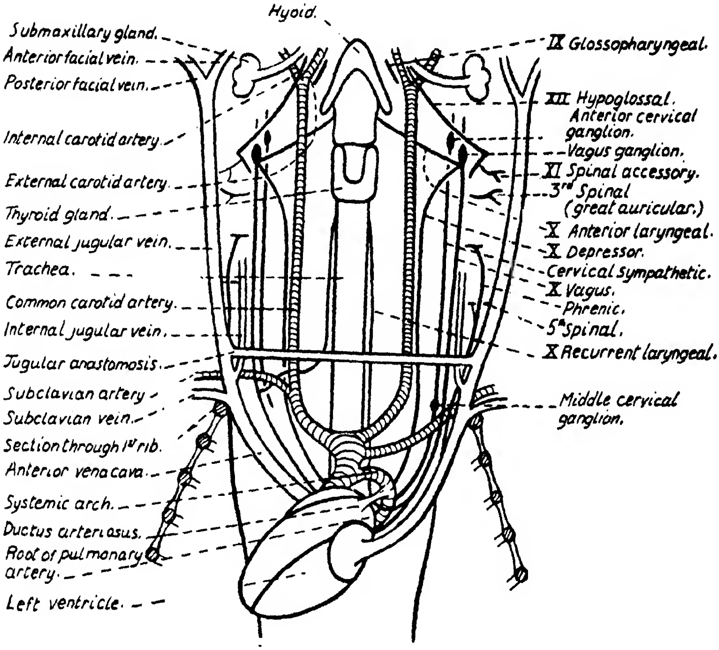


FIG. 24.36.—A slightly diagrammatic drawing of a dissection of the neck of a rabbit. The heart is deflected to the animal's right, and the arteries, veins and nerves are stretched laterally so as to increase the distance between them. All names on the right of the diagram are of nerves. Notice the asymmetry of the recurrent laryngeals and the origin of the arteries (cf. Fig. 24.26 and p. 447).

SENSE ORGANS: GENERAL FEATURES

The senses of a backboned animal, such as a rabbit, are more numerous than is generally realised. Besides the 'five senses' of sight, hearing, smell, taste, and touch, there are distinct kinds of sensibility to heat, cold, and the movements of the body, an indefinite general sensibility and a sense of damage to the tissues which in man is associated with the feeling of pain. Each of these senses has origin in impulses derived from a special kind of nerve ending, but only in the case of sight, hearing, and smell are these endings situated in a highly specialised organ. We shall here consider only these organs.

EYES

The eyeball of a mammal is best studied in that of the sheep or ox (Fig. 24.37); it is roughly spherical, but flattened on the front side. It consists of the following parts: (1) The outer coat or sense capsule corresponds to the auditory and nasal capsules, but fits closely to the eye instead of forming a hollow capsule fused to the skull. Over the greater part of the eye it consists of dense connective tissue with some cartilage and is known as the sclerotic, but on the front side it is transparent and known as the cornea. (2) The skin over the cornea adheres to it as a delicate, transparent covering, the conjunctiva, which is kept moist by the secretion of Harderian glands below the eye and lacrimal or tear glands above the outer corner of each eye. There are no Harderian glands in man. The secretions of these glands drain from the conjunctiva into the nose. (3) Inside the sense capsule is the choroid coat, consisting of looser and highly vascular connective tissue containing numerous dark pigment cells. In front the choroid thickens as the ciliary body and then separates from the sclerotic and passes inwards, as a partition called the iris, across the hollow of the eyeball, which it thus divides into anterior and posterior chambers. The former is smaller and filled with a watery aqueous humour, the latter larger and filled with a gelatinous vitreous humour. In the middle of the iris is an opening, the pupil, and the iris contains muscular tissue by which the size of the pupil can be altered. (4) Immediately behind the iris lies a firm, transparent body, the lens, which serves to focus upon the sensitive surface at the back of the eye the light which enters through the pupil. (5) The sensitive surface is provided by the retina, a delicate membrane containing two primary layers, an outer pigment layer of pigmented cells lining the choroid, and an inner retina proper which has at the back of the eye a very complicated structure (Figs. 26.30, 26.31) and is connected with the optic nerve, by which the impulses which give rise to sight are conveyed to the brain. The fibres of the optic nerve pass right through the retina and spread out over its inner surface (that which is turned towards the hollow of the eyeball). The percipient cells are on the outer surface, against the pigment layer, so that light must pass through the layer of nerve fibres to reach them. Where the nerve leaves the eye there are no sense cells, so that there is a blind spot; the fovea is an area of special acuity,

on which images are normally focused. In the front half of the eye the retina loses its complicated structure and becomes very thin, but it continues to line the posterior chamber up to the edge of the pupil.

For an object to be seen it is necessary that an image of it should be formed on the retina. The formation of such an image

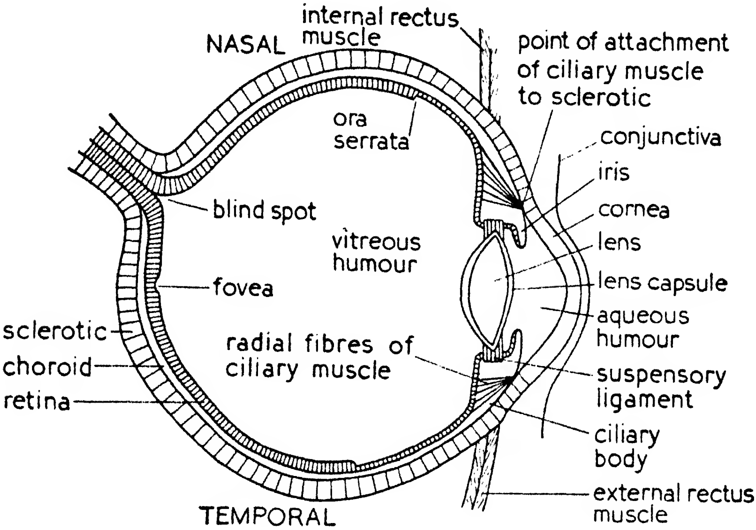


FIG. 24.37.—A diagrammatic horizontal section of a mammalian eye. The thickness of the choroid and retina, and especially of the anterior continuation of the latter over the posterior surface of the ciliary body and iris, is exaggerated.

is due mainly to refraction of light by the lens, but refraction also takes place at the surfaces of all the other media (cornea, aqueous humour, vitreous humour) through which the light passes in the eye. In the diagram below (Fig. 24.38) these effects are combined and the refraction shown as taking place at a single surface (p) situated in the aqueous humour. Each point of the object may be considered as sending out a pencil of divergent rays which by refraction are made to converge again into a point in an image which is constituted by such points corresponding to those of the object. The diagram shows that the image is inverted—what is the upper part of the object is represented in the lower part of the image and what is on the right-hand side of the object by the left-hand side of the image. The young organism has to learn to associate stimulation of a particular

part of the retina with objects that lie in a certain direction in space relative to the body and so is not inconvenienced by this inversion. Without such experience the retinal image could not be interpreted, and there is no question of the image being ' re-inverted ' by the brain, as is often supposed. The mammalian eye is able to focus objects that stand at varying distances from the eye—from infinity down to ten inches in a healthy adult man, and to even less in a child. This it does by altering the shape, and so the focal length, of the lens. At rest the lens is adjusted to focus distant objects, i.e. it is at its thinnest. It is held thus by the tension of the radial suspensory ligaments which hold it to the ciliary body. To focus nearer objects, ciliary

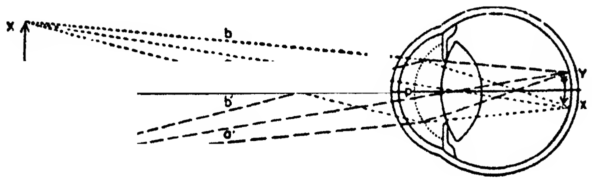


FIG. 24.38.—A diagram to show the formation of a retinal image.

a, *b*, *c*, Rays proceeding from the point X ; *a'*, *b'*, *c'*, rays proceeding from the point Y ; *p*, theoretical ' principal surface,' at which the combined refraction caused by the several surfaces of the eye is supposed to take effect. The lens is shaped as in man and the rabbit.

muscles contract, and in so doing reduce the tension on the ligaments. This allows the elasticity of the capsule which encloses the lens to come into play, and it makes the lens fatter, and so reduces its focal length. This adjustment of the eye to objects at different distances is called accommodation.

EARS

Something of the structure of the ear has already been incidentally mentioned (p. 426), and more is shown in Fig. 24.39. Sound waves are probably collected by the pinna, and certainly pass down the outer ear or external auditory meatus to the tympanum or eardrum. This vibrates, and transmits its vibrations to the chain of ear ossicles, the malleus, incus, and stapes, in the middle ear. The last of these pushes in and out against the membrane of the fenestra ovalis, and so causes pressure differences in the fluid called perilymph surrounding the sensitive parts of the inner ear, which themselves contain endolymph.

Muscles attached to the ossicles reduce their movement on receipt of a loud sound, so that there is some automatic volume control. The Eustachian canal, which leads from the middle ear to the pharynx, prevents excessive differences of pressure on the two sides of the tympanum. Its pharygeal end is normally closed, but opens in the act of swallowing. The part of the ear sensitive to sound is the cochlea, a long spirally-coiled tube which starts

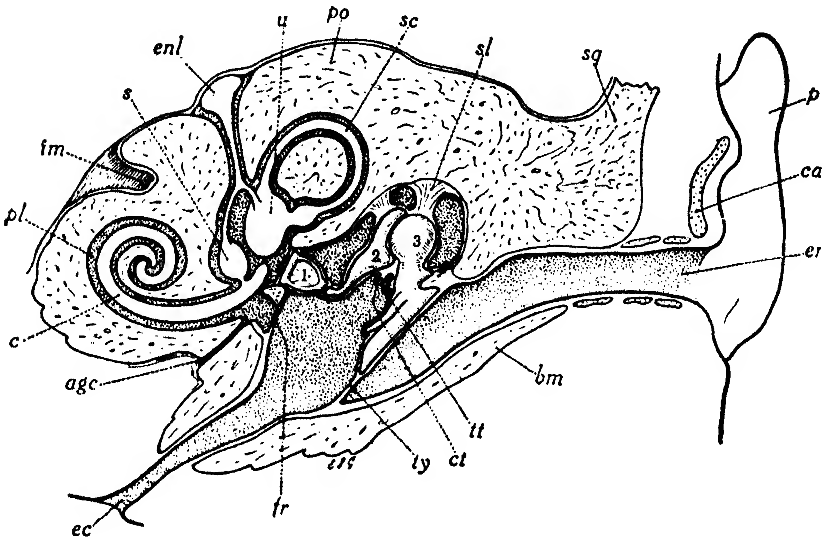


FIG. 24.39.—Diagram of ear of mammal in vertical section.—From Goodrich, *Studies on the Structure and Development of Vertebrates*, 1930. Macmillan, London.

agc., Aquaeductus cochleæ ; *bm*, bony meatus ; *c*, cochlea ; *ca*, cartilage ; *ct*, chorda tympani ; *ec*, Eustachian tube ; *em*, external meatus ; *enl*, saccus endolymphaticus ; *fr*, fenestra rotunda ; *im*, foramen for auditory nerve ; *p*, pinna ; *pl*, perilymph ; *po*, periotic ; *s*, sacculus ; *sc*, semicircular canal ; *sl*, suspensory ligament ; *sq*, squamosal ; *tt*, attachment of tympanic muscle ; *ty*, tympanum ; *u*, utriculus ; 1, stapes ; 2, incus ; 3, malleus.

from the sacculus. It is divided internally by membranes into three chambers, which are shown diagrammatically in Fig. 24.40. The upper, the scala vestibuli, is closed by the fenestra ovalis, and communicates at its other end by a narrow passage, the helicotrema, with the lower chamber, the scala tympani, which is shut off from the middle ear by the membrane of the fenestra rotunda. These two chambers contain perilymph, and the variation in pressure set up by the movements of the stapes are damped by the resistance of helicotrema and fenestra rotunda. The middle chamber, or scala media, contains endolymph, and its lower wall, the basilar membrane, bears the organ of Corti. This consists of

a number of hair-like processes connected with branches of the auditory nerve, and it is these which respond to the vibrations of sound. Quality, pitch and loudness can all to some extent be distinguished. The ability to determine the direction from which a sound comes depends largely on the phase-difference between the waves arriving at the two ears. The utriculus and the three semi-circular canals (two vertical, one horizontal) are organs of balance. They are known collectively as the pars superior of the labyrinth,

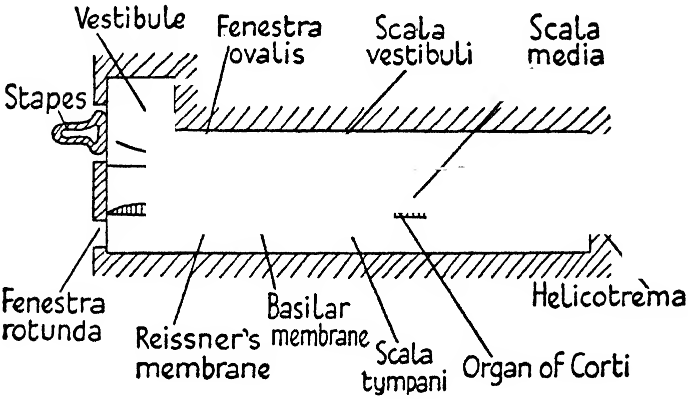


FIG. 24.40.—A very diagrammatic representation of the mammalian cochlea, unwound. Diagonal shading indicates bone. The stapes is in the middle ear, and the fenestra rotunda also looks into this space.—From Yapp, *An Introduction to Animal Physiology*, 1939. Clarendon Press, Oxford.

and each labyrinth consists of a bony cavity enclosing a membranous one, on the inner walls of which are sensitive endings of the eighth cranial nerve. Varying pressures on these, caused by changing position or movements of the head, cause compensatory reactions of muscles of the eyes and body, so that there is a general tendency for the animal to remain upright. The utriculus is concerned chiefly with static reactions and linear accelerations, the canals with angular accelerations. The ductus endolymphaticus runs from the sacculus to a small expansion under the brain.

OTHER SENSES

The olfactory sense cells are situated in the Schneiderian membrane which lines the olfactory chambers (p. 426). They

respond to air-borne particles of chemical substances. Minute sense organs of taste, known as taste-buds, are found in various parts of the mouth, principally on certain elaborate papillæ of several kinds on the tongue, and are supplied with fibres which run in the glossopharyngeal nerve and in the mandibular branch of VII. The nature of the sense of taste in the rabbit, though perhaps not in lower animals, may be inferred from that of man. In man the only true 'tastes' are the perceptions of the qualities sweet, sour, bitter, salt, and perhaps metallic and alkaline. Other so-called tastes are aromas perceived by the organ of smell, to which traces of the substances that give rise to them are conveyed by air from the mouth through the posterior nares. The rabbit has also sense cells in the skin which are sensitive to touch and temperature, and in the muscles which respond to their tension and so enable the animal to maintain its tone and its posture and gait.

HORMONES

Another method of control and co-ordination, which is found in all vertebrates and in some of the more advanced invertebrates such as arthropods and molluscs, is by hormones or chemical messengers. These are substances which are produced in the body and released into the tissues (typically into the blood stream) whence they are carried or diffuse to one or more other parts of the body, on which they have either a specific or a general effect. They may be produced either in ordinary glands (though usually in specialised parts) or in the specialised endocrine or ductless glands.

Good examples of specific hormones are those that control digestion. When food arrives in the stomach it causes the production of gastrin by the pylorus, and this stimulates the flow of pepsin. Pancreozymin and secretin similarly produced by the cells of the intestine, when peptones and acid respectively enter it, cause activity of the pancreas, the first stimulating it to produce enzymes and the second bicarbonate ; the acidity of the intestine is thus under automatic control.

The main part of the pancreas is a diverticulum from the gut that produces enzymes, but it contains also tissue, the islets of

Langerhans, that produces two hormones which help to control blood sugar.

The thyroid is a thin red body consisting of two lobes, one at each side of the larynx, joined by a band across the ventral side of the latter ; it begins as a single diverticulum from the pharynx. Its hormone is an excellent example of one of general effect ; its exact chemical nature is not certainly known, but it is related to the substance thyroxine which has been extracted from the gland, and is probably this substance united to a protein. It is continually being formed, and is necessary to maintain the activity of the body ; it seems to determine the basal metabolic rate (i.e. the rate at which oxygen is used in the absence of any special activity) and although its secretion probably varies little, the increased metabolism of fevers and on exposure to low temperatures may be caused by excess of it.

The thymus consists of two masses in front of the heart, derived in development from the epithelium of the gill slits. It has long been suspected to be an endocrine gland, but its function is obscure. It is much larger in young animals than in adults.

The pituitary is attached to the floor of the thalamencephalon (Fig. 24.33) and is almost surrounded by an upgrowth of bone from the basisphenoid making the sella turcica. Its anterior lobe, and part of the posterior lobe, are formed from an upgrowth from the roof of the mouth, the hypophysis, though the connection is early lost, while the rest of the posterior lobe comes from the infundibulum, a downgrowth of nervous tissue from the floor of the brain.

The anterior pituitary produces several hormones, of which the chief are the growth hormone, excess of which leads to gigantism, and especially to an extreme size of hands, feet, and jaws known as acromegaly, and the gonadotropins, which, as described on page 674, co-operate with the sex hormones to control the reproductive cycle.

Hormones from the posterior lobe have somewhat obscure effects on the kidney and on smooth muscle. They cause a reduced production of urine and initiate the flow of milk from the breasts of suckling mammals.

The suprarenals or adrenals can be seen as two small bodies, one in front of each kidney (Fig. 24.35). Each has two parts, an inner medulla, the suprarenal proper, which is derived from the

same set of cells in the neural crest (p. 654) as the sympathetic system, and the cortex, which is derived from the mesoblast of the kidney rudiment. The adrenaline produced by the medulla is another general hormone, but its activity is most marked when some special stimulus—low temperature, lack of oxygen, or (in man) the emotional states of fear or anger—causes its output to rise. It then has the same effects as stimulation of the sympathetic system ; these include a rise in blood pressure, dilatation of the pupil, erection of hairs, and breakdown of glycogen to lactic acid. Hormones from the cortex, collectively called cortin, help to control the concentration of sugar and sodium in the blood.

The testes and ovaries not only form spermatozoa and ova but also liberate hormones, of which some influence the development of secondary sexual characters in the growing individual, and others, co-operating with the pituitary, control the reproductive cycle as described on page 674.

It is clear that hormones are less well adapted to precise connections than the nervous system, and in fact most of them affect structures in more than one part of the body. It is necessary that hormones should be readily diffusible and easily destroyed, or they would be too slow in action and would persist after their effects were no longer required. In fact they are all of relatively low molecular weight and are rapidly destroyed in the body. Thyroxine is the only one which is not digested in the gut. It is probable that they take part in chemical reactions in the body, either as enzymes or as coenzymes. It is in fact difficult to frame a definition which will separate them from enzymes in general, and they differ from vitamins only in that they are made in the body, while vitamins must be taken in with the food ; what is a vitamin for one species may be a hormone for another.

In view of the fact that part of the action of the nervous system depends on the liberation of chemical substances, sometimes called neurohumours, it is tempting to think that a single primitive co-ordinating system has evolved along two lines, one ending in the vertebrate endocrine system, the other in the vertebrate brain. The adrenal medulla, which is formed from cells of nervous type, remains as a link, for its secretion adrenaline is similar to, and possibly identical with, the sympathin liberated by the ends of sympathetic nerve fibres ; as we have seen, the two substances have the same effects.

THE RAT

The laboratory rat, a cage-bred variety of the brown or Norway rat, *Rattus norvegicus*, is often dissected as a mammalian type instead of the rabbit. It is now considered to belong in an order, the Rodentia, distinct from that called Lagomorpha in which the rabbit is placed, but the two species do not differ fundamentally. The chief points of difference which the elementary student might notice in dissection are listed below; there are also some differences in the skeleton, which is seldom studied.

External features. In addition to obvious differences of shape and form, the big toe is present; there are usually six pairs of teats, three pectoral and three abdominal.

Alimentary system. The tonsils are absent, or perhaps are represented by scattered pits in the throat. The dental formula is $\frac{1\,0\,0\,3}{1\,0\,0\,3}$. There is no infraorbital salivary gland, but there is a major sublingual lying on the anterolateral surface of the submaxillary gland, and a minor sublingual beneath the mucous membrane on the floor of the mouth. The pancreas is more diffuse than in the rabbit, and extends into the omentum which joins the spleen to the stomach. There is no gall-bladder. The cæcum differs considerably from that of the rabbit; it is relatively shorter, it does not show the well-marked three limbs, and it is not spirally constricted. It is divided about the middle by a slight groove, which marks off the distal part as the appendix.

Circulatory system. The cœliac artery divides into three, the gastric, splenic and hepatic. The iliolumbar arteries usually arise from the dorsal aorta; the posterior mesenteric artery arises from a point near the origin of the iliac arteries. The internal and external jugular veins open separately into the anterior vena cava; there is a small anastomosis between the internal jugular veins but apparently none between the external veins. The azygos vein is on the left side and enters the left anterior vena cava. There is one pulmonary vein from each lobe of the lung, that is, one on the left, four on the right. There is a single hepatic vein. The external iliac vein and the elements of the internal iliac or hypogastric usually join to form a common iliac.

Urinogenital system. Near its opening each vas deferens gives off a large seminal vesicle or vesicular gland. There is no evidence

that it stores sperms, but its secretion adds much bulk to the semen, and it secretes the fructose on which the sperms feed.

Nervous system. The brachial plexus is formed from the first thoracic and last four cervical nerves, with usually a small branch from the second thoracic. There is a lumbosacral plexus formed from all six lumbar nerves and the first sacral.

25

MAMMALS

We have studied the rabbit as an example of a mammal, and in this chapter we shall consider the class Mammalia as a whole. In spite of the relatively small numbers of species (Britain has about fifty, while there are nearly two hundred resident birds and some twenty thousand insects) its members have been extraordinarily successful in colonising almost all parts of the globe, largely because their constant temperature makes them to a great extent independent of the weather, and because their brain makes them able to learn by their experience and modify their behaviour in an unprecedented way. The mammals of different environments have different details of structure which on the whole are obviously connected with habit or habitat ; thus otters, which swim, have webbed feet, and many monkeys, which climb, have prehensile tails. The existence of such 'adaptations' is now considered evidence that all the mammals have evolved from the same ancestors (Chap. 30), and such divergence of descendants is known as adaptive radiation. Most groups of animals show such radiation, and it is a useful intellectual exercise for the student, having studied it in mammals, to try to apply the principle to other animals which he knows. The more successful a group is, the more likely is it to show clear adaptive radiation ; the insects and birds are therefore easy to work out. It should be noted that adaptive radiation is best seen in external features, since these have a closer dependence on the external environment than has the internal structure.

In formal terms the mammals are not easy to separate from reptiles, but for practical purposes an animal is easily recognised as a mammal if it has hair, or, should only the skeleton be available, if it has a lower jaw consisting of a single bone on each side, or in dissection if it has a muscular diaphragm. The majority of existing mammals have also two other features which are possessed by no other animals—a placenta formed from the allantois, and mammary glands, which are vestigial in the male but in the female produce milk on which the young are fed. Mammals which possess both these features are called Eutheria or Placentalia. The British Isles contain examples of almost all

the chief orders of placentals, although some of them are present only in the domesticated state; one exception must in fact be made to the generalisation given above about the success of mammals, for they have not stood up well to the impact of civilised man. The largest wild mammal which has maintained itself in Britain without protection is the badger, of weight about twenty-five pounds, and it is remarkable that two of the most successful species, the brown rat and the rabbit, are human importations which are not native to the country. The birds, although they also have lost many of their larger species, have suffered much less. Most of the more successful mammals are small, unobtrusive and nocturnal, and survive, like hedgehogs in suburban gardens, largely because they are seldom seen.

The orders of eutherian mammals are put into four main groups, which may be called cohorts; each cohort may be assumed to be descended from what was, at the time when the placentals were becoming established, a single order. The first of them is the Unguiculata, or nailed animals, which have mostly retained a primitive internal structure with many features reminiscent of reptiles. Great Britain has examples of three orders, the Insectivora, Cheiroptera, and Primates.

INSECTIVORA

There is no vernacular English name for the insectivores; their Latin name means 'insect-eating', but it is important to remember that 'insect' here has the meaning which it has for the populace, not that which it has for zoologists. An insectivore may feed on insects, on other arthropods, on snails and slugs, and on worms; some, such as hedgehogs, also take small vertebrates and some vegetable matter.

There is no peculiarly insectivore character, but the order is notable for possessing many features which are believed to be primitive; that is, features which are found in the earliest fossil mammals, or in reptiles, or in both. The cranial cavity is small, the tympanic bone is ring-shaped, and the palate is fenestrated, that is, full of holes. The teeth are often what is considered to be the full set, with formula $\frac{3\,1\,4\,3}{3\,1\,4\,3}$, and the crowns of the cheek teeth have a small number of sharp-pointed cusps. There is a clavicle and usually a centrale, and the radius and ulna

remain separate. There are generally five digits on each limb and the animal walks with the palms and soles on the ground, and so is called plantigrade. The brain is of very reptilian type, with large olfactory lobes, and the specially mammalian features of corpus callosum and neopallium poorly developed. Other primitive features are found in the reproductive system ; there is often a cloaca, the uterus is primitive and often duplex, that is, the right and left tubes are separate, and join only in a median vagina, and the testes, although they shift backwards from their original position, do not descend into a proper scrotum. Another link with the reptiles is found in the fact that the constant body temperature is not permanently established, since many insectivores hibernate and in so doing become cold-blooded.

The insectivores, however, are not mere primitive mammals, for nearly all of them show specialisations of one sort or another. Although they are all small and retiring in habits, and mostly nocturnal, they have exploited their environment in various ways. The hedgehog (*Erinaceus europæus*), with its spines and habit of rolling into a ball when touched, has achieved a high degree of freedom from enemies ; it has also peculiar teeth, for the first incisors are long and 'caniniform', that is, they resemble the canine of a dog. The mole (*Talpa europæa*) is highly specialised for a digging or fossorial life. Its fore-limbs are greatly strengthened and the palms are turned backwards, so that they have become paddles for digging ; the eyes are small and almost or perhaps quite functionless, the pinnæ are vestigial, and the fur is short and lies equally well in all directions. The remaining British insectivores, the shrews (Soricidæ), are less obviously specialised, but they have an elongated snout, associated with hook-like first upper incisors and long and horizontal first lower incisors, and they have lost the zygomatic arch. They are rather more than insectivorous, since they kill and eat small rodents, even those larger than themselves. They include the smallest known mammals, the pigmy shrew, *Sorex minutus*, of Britain being one of the least. Its length, apart from the tail, does not exceed sixty millimetres nor its weight six grammes. Because of their large surface area in proportion to their volume their rate of loss of heat is high relative to their ability to produce it, and they must be continually feeding to supply food to be burnt. A fast of a few hours is fatal, except when they are hibernating and they have ceased to be warm-blooded.

CHEIROPTERA

The bats show many primitive features which relate them to the insectivores, such as the possession of five digits, small cerebral hemispheres, and undescended testes, and often of a duplex uterus. Their command of warm blood is imperfect, for their temperature falls to that of their surroundings whenever they are inactive. On waking, they restore their warm-blooded state by muscular activity. Their chief specialisation is obviously the possession of the power of true flight, in which they are unique amongst mammals. Their wing is a patagium or fold of skin stretched from the second finger to the tail and supported chiefly by the radius, the second to fifth metacarpals, and the tibia. There are many specialisations in the skeleton ; not only is the hand enormously enlarged, but the ulna is reduced and fused to the radius, the clavicle is large, and the sternum bears a keel, although this is small compared with that of birds. The pelvic girdle has long ilia and is attached to a long, strong sacrum, but there is only a loose ventral symphysis, or none at all ; there is little movement between the vertebræ, and the ribs are flattened and form a rigid thorax. It will be noted that although the structure of the wing skeleton is very different in the birds and in the bats (Fig. 30.8), the other skeletal peculiarities are very similar, and look as if they were either produced by, or were a necessary condition for, successful flight. Other features of obvious importance in flight are the large heart and lungs. The first digit of the fore-limb and all those of the leg bear claws, by means of which the animal can hang ; it spends most of the day hanging upside down by its toes, and hibernates in the same position. The bats share with a number of other mammals a peculiar separation of the season of sexual activity and birth, for which no satisfactory explanation in terms of function is known. In the bats copulation occurs in the autumn, but the sperms are stored within the female until spring, when fertilisation occurs. Another peculiarity is the great sensitivity of their hearing and the use to which this is put. When flying, they avoid obstacles—and they are notoriously good at doing this—by making high-pitched squeaks and picking up the echoes which are returned from solid objects. As they can pick their way rapidly between quite complicated sets of wires their co-ordination must be both rapid and good.

All the British species belong to a section of the Order, the Microcheiroptera, which feed on insects caught on the wing and have cheek teeth much like those of the Insectivora. There are twelve British species, but only two of these, the pipistrelle (*Pipistrellus pipistrellus*) and the long-eared bat (*Plecotus auritus*) are widely distributed. In some species insects caught on the wing are transferred to a pouch, formed by the forwardly-turned tail, for storage.

PRIMATES

The primates resemble the Insectivora so closely that there has long been, and still is, controversy as to whether one family, the tree-shrews or Tupaiidæ, are best placed in one group or the other. These are small creatures from the Eastern tropics and differ from the typical insectivores in a number of features in which they agree with the primates. Primates are in fact fundamentally arboreal insectivores; they retain a number of primitive features such as tubercular cheek teeth, the clavicle, separate radius and ulna, plantigrade gait and five digits, but show a number of progressive specialisations. The orbit is surrounded by bone, the postorbital process of the frontal meeting an upgrowth from the jugal, there is a gradual reduction in the relative extent of the preorbital region of the skull, the claws become flat nails, and both hallux and pollex are typically opposable, so that first the branches of trees and then portable objects can be grasped. It has indeed been suggested that the development of the thumb was the most important step in the evolution of the order, for by its means, combined with stereoscopic vision, objects can be examined and so thought becomes directed to a particular thing and more readily used as the material for natural selection. It is relevant to this hypothesis that the parrots, which also use the feet as hands for holding and examining objects, have relatively the largest brains, and the largest cerebral hemispheres, of all birds. However that may be, the chief distinction of the primates is their large brains and their large and convoluted hemispheres. With this goes an increase in the carotid circulation.

So far as is known, the only primate ever to inhabit these islands is man, and the present species, *Homo sapiens*, probably arrived about fifty thousand years ago. While man retains such primitive

mammalian features as plantigrade gait and five toes, and signs of arboreal ancestry such as a large clavicle and the opposable thumb, he has his own specialisations, which are largely con-

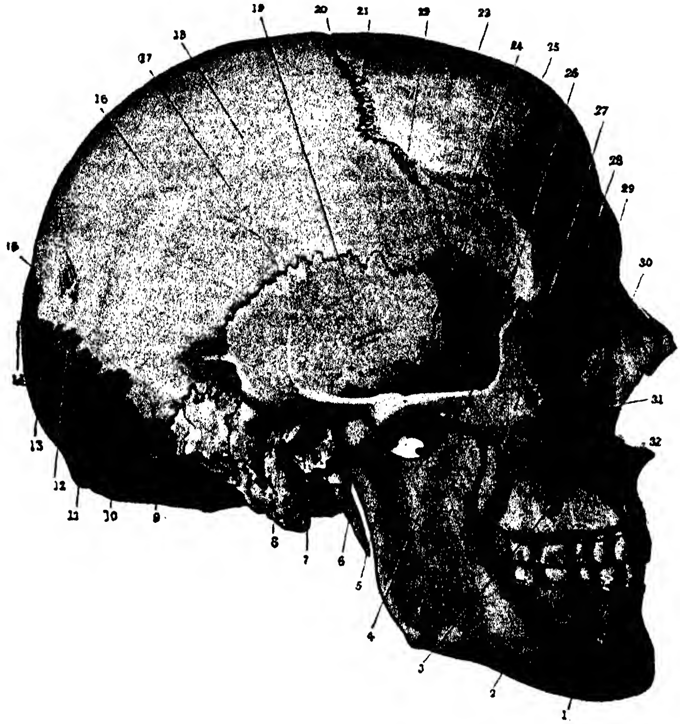


FIG. 25.1.—A human skull, seen from the right side.—From Cunningham.

1. Mental foramen.
2. Body of the mandible.
3. Maxilla.
4. Ramus of mandible.
5. Zygomatic arch.
6. Styloid process.
7. External auditory meatus.
8. Mastoid process.
9. Asterion.
10. Superior nuchal line of occipital bone.
11. External occipital protuberance.
12. Lambdoid suture.
13. Occipital bone.
14. Lambda.
15. Obelion placed between the two parietal foramina.
16. Parietal bone.
17. Lower temporal line.
18. Upper temporal line.
19. Squamous part of temporal bone.
20. Bregma.
21. Coronal suture.
22. Stephanion.
23. Frontal bone.
24. Pterion.
25. Temporal fossa.
26. Great wing of sphenoid.
27. Zygomatic bone.
28. Zygomatico-facial foramen.
29. Lacrimal bone.
30. Nasal bone.
31. Infra-orbital foramen.
32. Piriform aperture and anterior nasal spine.

nected with the upright stance. To make the best of his nine-pin-like shape and consequent unstable equilibrium he has developed a sigmoid curve in the backbone, the large gluteal muscles of the buttocks to prevent the body falling inwards when he stands on one leg, and the arch of the foot, with heel behind the point

of application of his weight, as well as a host of other modifications of musculature and skeleton. The opposability of the big toe has been lost, but that of the thumb has increased to a greater degree than is found in any apes; at the same time the radius can be rotated round the ulna (Fig. 24.20). There is a very high degree of tactile sensibility of the palmar surface, and an extraordinary sensitivity of the proprioceptors in the muscles and joints, so that we know without practice the position of the tip of the index finger, and the two index fingers can be made to meet blindfold in any position in space which they can reach.

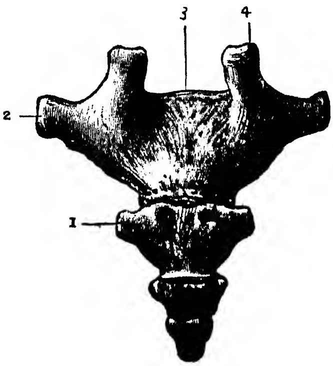


FIG. 25.2.—The coccyx, or vestige of the caudal vertebræ of man.—From Cunningham.

1, 2, Transverse processes; 3, for sacrum; 4, cornu.

The changes in the skull (Fig. 25.1) may be connected with the increased size of the brain, the adoption of a less actively carnivorous diet, and the upright posture. The brain case is greatly enlarged, the jaws are shortened, and the foramen magnum comes to lie underneath the skull. There is considerable fusion of bones; in the adult the four occipital bones and the interparietal form a single ring; the basisphenoid, presphenoid, alisphenoids, orbitosphenoids and pterygoids form a single sphenoid bone, which later ankyloses with the occipital; there is a single ethmoid, representing mesethmoid, turbinals and vomer; the periotic, squamosal and tympanic unite to form a temporal bone; and the premaxillo-maxillary suture almost or completely disappears. In the sutures of the cranium there may be small irregular Wormian bones. The projection of the dentary which forms the chin is a distinctive human feature. The dental formula is $\frac{2\,1\,2\,3}{2\,1\,2\,3}$; the canine, although it remains pointed, is only very slightly longer than the incisors, and the last molar, or wisdom tooth, quite often does not cut the gum. The pattern of the cheek teeth is bunodont, that is, there is a set of rounded cusps suitable for an omnivorous habit. Man has no tail, but three caudal vertebræ are present (Fig. 25.2).

One of the most striking features of man is his nakedness,

which suggests that his first home was in a warm climate, but for which it is difficult to conceive a function. There are, however, some signs of a tendency to lose hair in various monkeys, where use is made of bare coloured areas for sexual display. The chief peculiarity in man's soft parts is the size of his brain, and especially the great development and convolution of the cerebral hemispheres. With this goes his great mental development, in which he differs so much from all other animals as to give some justification for the opinion of his own uniqueness which he has long held. Young chimpanzees are at least the mental equals of

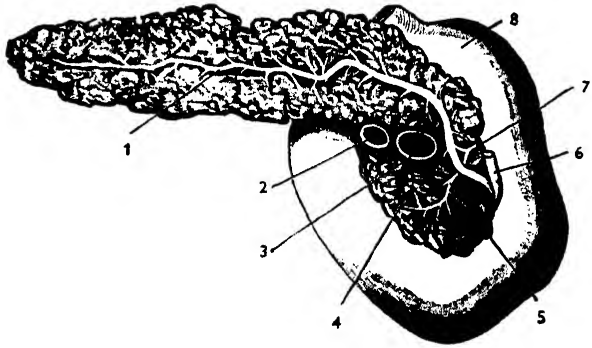


FIG. 25.3.—A dorsal view of the pancreas and duodenum of man, with the pancreatic duct exposed, showing its junction with the bile duct, and the accessory pancreatic duct.—From Cunningham.

1, Pancreatic duct; 2, superior (anterior) mesenteric artery; 3, superior mesenteric vein (branch of portal vein); 4, 'head' of pancreas; 5, branch of accessory pancreatic duct; 6, bile duct; 7, accessory pancreatic duct or duct of Santorini, communicating both with duodenum and with main pancreatic duct; 8, first (superior) part of duodenum.

children for the first year or two, but they soon cease developing and never progress beyond, at the most, the level of an average child of two or three. In language they are greatly inferior even to such a child. Much is sometimes made of the ability of man to think in terms of words and abstract concepts, but although this is common in the writers of books, it is by no means universal; even many books are, like abstract painting and the song of birds, expressions rather of an emotional state than of precise thought. The ability to reason, that is to foretell the probable consequences of actions which have not been carried out before, is presumably found in all normal men, but it is not always used. Anatomical differences are: in man the pancreatic duct joins the bile duct near the entry of the latter into the duodenum (Fig. 25.3); the vermiform appendix is a good deal

smaller and the cæcum very much smaller (Fig. 25.4) ; the left superior vena cava (or innominate vein) joins that of the right side

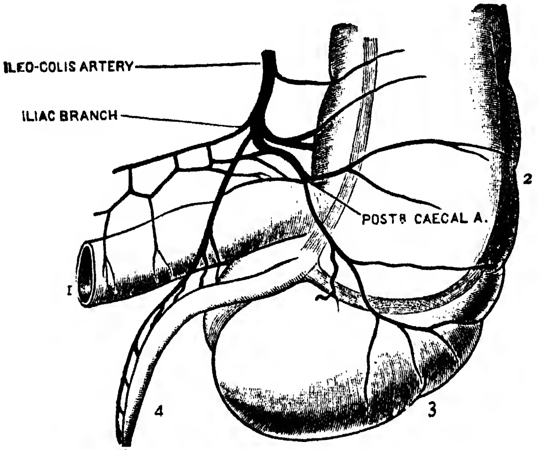


FIG. 25.4.—The cæcum and neighbouring structures in man.—From Cunningham.
1, Ileum ; 2, colon ; 3, cæcum ; 4, appendix.

before the latter enters the heart, forming thus a single superior vena cava ; the external and internal iliac veins on each side join to form a common iliac ; the fibres of the depressor branch of the tenth nerve are included in the main vagus trunk ; there is a single pair of mammæ, which are on the thorax ; the uterus is a single median structure (Fig. 25.5) ; the testes descend into an external scrotum ; a seminal vesicle opens into the hinder end of each vas deferens (Fig. 25.6) ; and the third eyelid is represented only by a slight semilunar fold of membrane, the plica semilunaris.

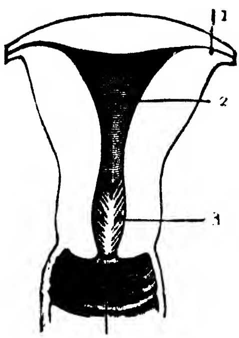


FIG. 25.5.—A diagram of the human uterus in longitudinal section. At the lateral angles the Fallopian tubes have been cut away. —From Cunningham.

1. Lateral angle of uterus ; 2, cavity of body ; 3, cavity of cervix ; 4, vaginal cavity.

FIG. 25.6.—The lower end of a vas (or ductus) deferens of man, with its seminal vesicle.—From Cunningham.

amp., 'Ampulla' of vas deferens ; *d.ej.*, ductus ejaculatorius ; *v.s.*, vesicula seminalis.

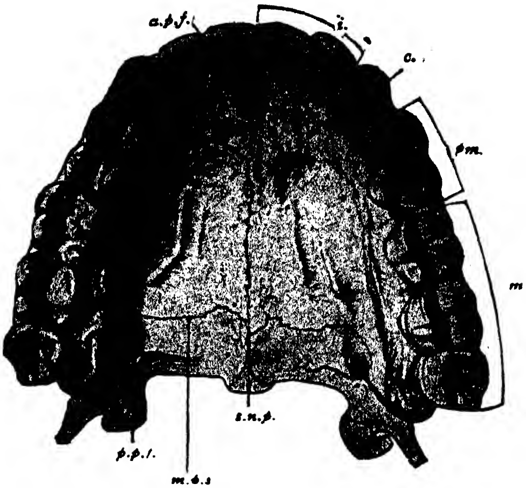


FIG. 25.7.—The bones of the hard palate and upper permanent teeth of man. *a.p.f.*, Anterior palatine foramen, or incisive foramen ; *c.*, canine tooth ; *i.*, incisor teeth ; *m.*, molar teeth ; *m.p.s.*, suture between maxillary and palatine bones ; *p.p.f.*, posterior palatine foramen ; *pm.*, premolar teeth ; *s.n.p.*, posterior nasal spine.

GLIRES

The second cohort of the placental mammals, called Glires, is coterminous with the old order Rodentia. They retain a number of primitive features, such as a small brain, five fingers and toes and plantigrade gait, and separate radius and ulna. Their chief adaptive features are the development of the teeth and jaws for gnawing, and an extreme fecundity, which is achieved partly by large litters and many of them in a year, and partly by an early sexual maturity. The result is that they can and do increase rapidly in numbers, but that the population becomes too large to be maintained and is drastically reduced by disease or other means. The result is cyclical fluctuation in abundance, the period being fairly constant for each species. Both in numbers of species and numbers of individuals the Glires exceed all other mammals. Fortunately they are always small. They were long kept together in a single order, but it is now considered that the two obvious subdivisions have only a superficial resemblance and they are therefore termed Orders, the Lagomorpha and the Rodentia in the strict sense. Even the placing of these in a single cohort is more a matter of convenience than of reason and some authors consider their adaptive resemblances to be entirely due to convergence ; both orders are certainly well isolated from all other mammals.

LAGOMORPHA

This order includes the rabbits and hares, and has been adequately illustrated in our study of *Oryctolagus cuniculus*. The incisors are developed for gnawing, but the large upper pair are backed by a smaller pair, hence the earlier name for the group of Duplicidentata. There is no canine, but a long diastema between incisors and cheek teeth. These last have sharp transverse ridges and are therefore called lophodont. There is much freedom of movement of the lower jaw, the articular surface of the squamosal being broad and flat. The animals are almost entirely herbivorous. The hind legs of rabbits and hares are elongated to give a semi-saltatorial or jumping type of locomotion and the tail is short. The only native British lagomorphs are the brown hare (*Lepus europæus*) of the lowlands and the blue or variable hare (*Lepus timidus*) of the Scottish Highlands. They are larger than the rabbit, but closely resemble it in structure. The chief differences are in habits and psychology ; hares do not burrow and are solitary, and the antics of the courting males in spring have led to the saying, ' Mad as a March hare '. The variable hare becomes white in winter. The rabbit was introduced into this country probably in the twelfth century.

RODENTIA

These, the Simplicidentata of older classifications, differ obviously from the Lagomorpha in possessing but a single pair of upper incisors. There are in addition so many differences of detail between the jaws of the two groups that the resemblance between them may be due to convergence, that is, the approach to a single result by two different routes. The incisors have enamel on the anterior surface only, and so become chisel-shaped by wear, the lophodont cheek teeth bite with the upper set inside the lower (the reverse of rabbits), and the two dentaries are not sutured. Instead, they can be drawn apart by muscles, and when this happens the lower incisors are pressed together ; when the antagonistic muscle pulls the mandibles together the incisors are separated, and by this alternating scissors action they can be used for holding or for separating small objects. This facility is perhaps connected with the fact that the hand is often prehensile, so that food is held to the mouth to be eaten. There is an

even greater freedom of movement of the articulation of the jaw than in the rabbit, and in particular the attachments of the muscles are shifted so that they can pull the jaw forward.

There is a great deal of adaptive radiation within the order, which includes land-living and burrowing forms, aquatic animals such as the beaver (*Castor fiber*), saltatorial kangaroo-like creatures such as the jerboas, the semivolant flying squirrels with a long patagium stretched from limb to limb, and the aberrant spiny porcupines. In Britain we have only some of the less remarkable species, chiefly the rats and mice. The genera *Mus* (house mouse), *Rattus* (black and brown rats), *Apodemus* (field mice) and *Micromys* (harvest mouse) make the sub-family Murinæ, with dental formula $\frac{1003}{1003}$ and cheek teeth with closed roots and a crown pattern of three transverse ridges. *Rattus* and *Mus* are both human importations to this country, and to some extent at least dependent on man for their continued existence. The house mouse (*M. musculus*) became extinct on St. Kilda a few years after the human population left. The black rat (*R. rattus*) was formerly important because its fleas, *Xenopsylla cheopis*, carried the germs of plague, as they still do in the East. The Microtinæ or voles have the same number of teeth as the mice, but the roots of the cheek teeth remain open permanently or until late in life. The crowns are worn flat by the food, which is largely grass, and show a characteristic pattern of transversely elongated triangles. The short-tailed or field vole (*Microtus agrestis*) is probably our most numerous mammal, but as it spends most of its time in runs which it makes in long grass it is seldom seen.

The dormouse (*Muscardinus avellanarius*) has dental formula $\frac{1013}{1013}$, and is notorious for the depth and length of its hibernation, during which it consumes much of its stored fat. Its European relative *Glis glis*, which was fattened for the table by the Romans on chestnuts and walnuts and served with honey sauce, has been introduced into England and is numerous in parts of Hertfordshire and Buckinghamshire. The dormouse is arboreal, and, as its specific name correctly implies, it inhabits chiefly the hazel trees, which make a second layer in so many oakwoods. More characteristically confined to the trees are the squirrels, of which the only native British species, the red squirrel (*Sciurus vulgaris*) seems to

be primarily an animal of the fir woods, which once covered most of Britain but now persist, otherwise than as plantations, only in some restricted parts of the Highlands of Scotland. It is not therefore surprising that the red squirrel is not a very successful species under present conditions. It has, however, increased in some districts in recent years. Squirrels are among the more primitive rodents, with dental formula $\frac{1023}{1013}$ and a more normal arrangement of the jaw musculature than the mice. The grey squirrel (*S. carolinensis*) was introduced from North America at various places from 1876 to 1910, and is now common in woods and parks over most of midland and southern England.

Several other species of rodent are known as fossils; the most remarkable is the beaver (*Castor fiber*), a large aquatic species notorious for its habit of building dams with carefully fitted logs of wood. It persisted in Wales into historic times.

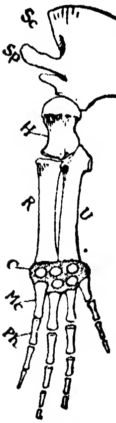


FIG. 25.8.—The left fore-limb of *Balænoptera*, a whalebone whale.—From Thomson.

Sc., Scapula with spine (*Sp.*); *H.*, humerus; *R.*, radius; *U.*, ulna; *C.*, carpals embedded in matrix; *Mc.*, metacarpals; *Ph.*, phalanges.

CETACEA

The third cohort, Mutica, contains only one Order, the Cetacea, or whales and dolphins, which, except that they still breathe air, have become completely aquatic. In so doing they have come to have considerable superficial similarity to fishes. They have the same streamlined shape, they swim by a caudal fin, and they balance by the fore-limbs and unpaired fins, but the flukes of the tail are horizontal instead of vertical, and neither they nor the unpaired fins contain any skeleton. That of the fore-limb, although reduced, is recognisable as coming from the pentadactyl type (Fig. 25.8). The teeth are with few exceptions either many, conical, peg-like and of a single set only, or completely absent; if they are present the animals are usually piscivorous, if they are absent the animals have returned to the microphagy of their early chordate ancestors (p. 303), and filter the water with combs made of baleen or whalebone, which is in fact keratin. Whales have a thick layer of fat or blubber beneath

the skin, and a number of pecularities in the respiratory system which help them to remain for several minutes under water, and to be active the whole time. They have lost a number of the usual mammalian characters, such as hair (except for a few bristles round the mouth), claws, pinnæ, all the muscles and glands of the skin, the scrotum, salivary glands, and the clavicle. The only trace of the pelvic girdle and hind limb is a small bone representing the ischium. The blue whale (*Balænoptera musculus* = *B. sibbaldi*), which is the largest known animal, living or extinct, and may be

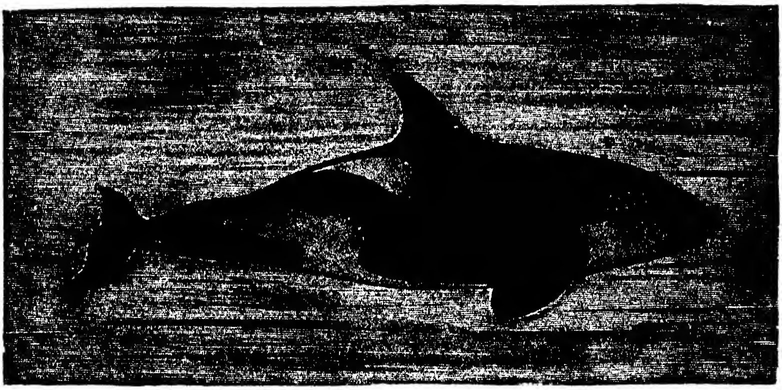


Fig. 25.9.—The killer whale (*Orca gladiator*).—From Beddard, after True.

as much as 100 feet long, has occurred in British waters, but most of those commonly seen round our coasts are much smaller. Such is the porpoise (*Phocæna phocæna* = *Ph. communis*) four to five feet long, which swims and gambols in schools following the herring and other small fish, and is often seen from the shore.

FERUNGULATA

The last cohort, the Ferungulata, contains a number of orders which, although now diverse, show distinct similarities in some of the fossil forms. It includes the four orders formerly included under the now abandoned name Ungulata, or hoofed animals, several extinct and minor orders, and the Carnivora, with which we will begin.

CARNIVORA

The typically flesh-eating animals are the nearest to the central stock of the cohort, and through their ancestors the creodonts

can be traced back to the ancient insectivores. Although, with one or two exceptions, all modern Carnivora are carnivorous, they exercise the habit in different ways; there are therefore several different radiations within the main line, and it is difficult to choose a typical animal for description. The dog (*Canis familiaris*) may, however, be taken as a central example, more carnivorous than the bears but less so than the cats. Its skull has already been described (pp. 423–31) and shows the typical large canine, small incisors and cutting (sectorial) cheek teeth, with the highly developed carnassials; the roller articulation of the jaw, preventing lateral motion, is also noteworthy. Other features of the skeleton are the raising of the feet, so that the animal is digitigrade and walks on the distal phalanges, and the absence of the clavicles. The limbs, like the jaws, have little lateral motion. The brain is relatively large, and hearing and smell are good; sight, however, is by human standards poor, though probably at least as good as in most mammals. Primitive mammalian features are the separate forearm and shin bones, the presence of five toes on the fore-limb and four on the hind, and a bicornuate (that is, forked) uterus. The stomach is simple and the cæcum small.

The origin of the domestic dog is unknown, but fossil remains suggest that he was an early companion of man. The wolf (*Canis lupus*) was abundant in Britain in the Middle Ages, but became extinct in England about the end of the fifteenth century, and in Scotland in the eighteenth. The fox (*Vulpes vulpes*), which is similar in general structure to the dog, is common over most of Britain, but owes its survival, at least in the lowlands, to protection.

The cats (family Felidæ) are more strictly carnivorous than the dogs, which feed largely on carrion and sometimes take vegetable matter. They have smaller incisors, fewer and sharper cheek teeth, relatively longer canines (dental formula $\frac{3\,1\,3\,1}{3\,1\,2\,1}$), and the claws are sharper and are normally held retracted into sockets so that they do not touch the ground. This feature, as well as the presence of a small clavicle, may be connected with the frequent arboreal habit. Besides the domestic *Felis catus*, which probably originated in Egypt and is perhaps a hybrid, there is in Britain the wild cat (*F. silvestris*), now confined to the Highlands of Scotland. Its food consists of relatively large animals, such as grouse and blue hares.

At the other extreme are the bears (Ursidæ), which are

plantigrade and have lost the carnassials and acquired crushing bunodont cheek teeth. They are largely herbivorous in diet. The brown bear (*Ursus arctos*) disappeared from the British fauna probably about the tenth century.

The remaining British land carnivores all belong to the family Mustelidæ, which is somewhat intermediate between the dogs and the bears. The badger (*Meles meles*) is plantigrade and has crushing molars. It is partly carnivorous, but largely digs for inactive prey such as young rabbits, and also takes much invertebrate and vegetable food. The weasel (*Mustela nivalis*), stoat (*M. erminea*), polecat (*M. putorius*), and marten (*Martes martes*) are in general similar and form a series ascending in size in the order given. All are active hunters, feeding on other mammals and birds, and at least to some extent arboreal. They are completely or partially digitigrade, with partially retractile claws, and although the molars are crushing the canines are sharp. The weasel and stoat are common, but the other two are confined to the mountains. Northern stoats become white in winter, when their fur is ermine, but the change seldom happens in England. The last member of the family, the otter (*Lutra lutra*), is aquatic and piscivorous, living chiefly in rivers but also on the seashore. It takes also shellfish and occasionally land animals. The cheek teeth are pointed and suitable for holding, not crushing. The shoulders are inconspicuous and the feet webbed, but not quite completely.

The seals and walruses are Carnivora which have become almost completely aquatic, although they still come to land for copulation and parturition, as well as for rest. The cheek teeth are either peg-like, or have three points in a longitudinal row, so that they approach the condition of those of the toothed whales and are suitable for holding fish. The fore-limbs are reduced to flippers, by means of which swimming is carried out and a jerky but surprisingly rapid movement is possible on land, and in all the normal British species the hind-limbs are held permanently backwards alongside the tail. Six species are recorded as being found on British coasts, the commonest being *Phoca vitulina*, which is one of the smaller sorts, about four or five feet long.

Many of the Mustelidæ, such as the stoat and the badger, agree with the bats in having a long interval between copulation and birth, but here the pause is brought about in a different way. Fertilisation occurs at once, and segmentation begins,

but the blastocyst (p. 668) stops its development and remains free in the uterus throughout the winter. In the spring, development continues, and a placenta is formed in the usual way.

PERISSODACTYLA

No members of this order are wild in Britain to-day, and as it includes only the horses, rhinoceroses and tapirs, it must be

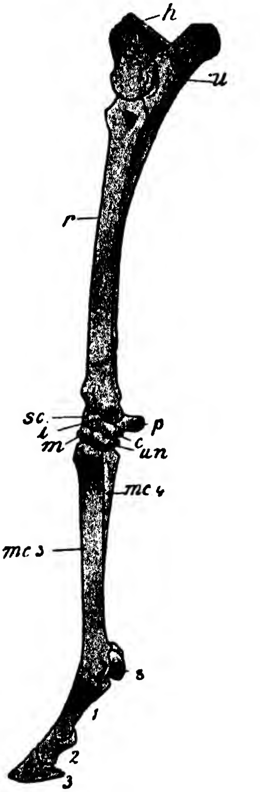


FIG. 25.10.—A side view of the lower part of a pony's foreleg.—From Thomson.

h., Distal end of humerus; *u.*, olecranon process of ulna; *r.*, radius; *sc.*, scaphoid; *l.*, lunar; *c.*, cuneiform; *m.*, os magnum; *un.*, unciform; *p.*, pisiform; *mc.*4, splint of fourth metacarpal; *mc.*3, third metacarpal; *s.*, sesamoid; 1, 2, 3, phalanges of third digit.

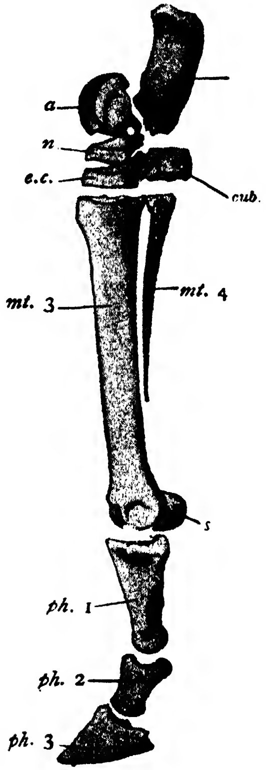


FIG. 25.11.—A side view of the ankle and foot of a horse.—From Thomson.

a., Astragalus; *c.*, calcaneum; *n.*, navicular; *e.c.*, external cuneiform; *cub.*, cuboid; *mt.*3, third metatarsal; *mt.*4, splint of fourth metatarsal; *s.*, sesamoid; *ph.*1–3, phalanges of third digit.

considered a relatively unsuccessful group. Its members are herbivorous, and the legs are lengthened for speed so that the animal walks not merely on its toes but on its nails, so that it is called unguligrade. The emphasis in the limbs is on the middle digit, so that when, as is usual, the digits are reduced, their number tends to be odd. In the modern horse (*Equus*, Figs. 25.10, 25.11), this reduction has continued until only a greatly enlarged third toe is left, with small functionless splint bones representing the second and fourth metacarpals and metatarsals ; there are other modifications for a rapid fore-and-aft movement of the limbs, such as

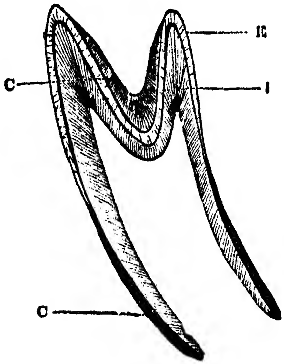


FIG. 25.12.—A vertical section of an incisor tooth of a horse.—From Theobald, after Chauveau.

C, Cement ; *E*, enamel ; *I*, dentine.

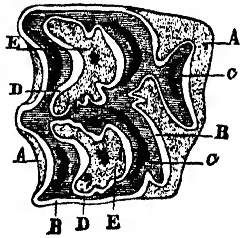


FIG. 25.13.—A transverse section of an upper molar tooth of a horse.—From Theobald, after Chauveau.

A, External cement ; *B*, external enamel ; *C*, dentine ; *D*, internal enamel ; *E*, internal cement.

pulley-like joints, reduction of the ulna and fibula to mere vestiges, and absence of the clavicle. The incisors (Fig. 25.12) slope forward and are used for cropping, the canine is reduced, and generally absent from the mare, and the cheek teeth (Fig. 25.13) have a complicated pattern produced by wear. The stomach is simple, but bacterial digestion of cellulose takes place in the cæcum and large intestine.

The orders Hyracoidea (the conies of the Old Testament, but not those of Elizabethan writers and the law, which were rabbits), Proboscidea (elephants), and Sirenia (sea cows) have no living British representatives. The conies superficially resemble rabbits, from which they can be distinguished by the triangular section of the upper incisors. The chief features of an elephant are its large size, its trunk, which is an elongated and prehensile nose and

upper lip (foreshadowed in the tapirs) and the teeth. There is a single pair of long upper incisors, the tusks, which are used in fighting and digging, and otherwise only a reduced number of cheek teeth, which replace each other throughout life like those of the dogfish. Each is very large, and only one and a half in each quarter of the jaw are in use at any one time.

ARTIODACTYLA

These, the 'even-toed ungulates', are by far the most successful of the larger herbivores, and include cattle, sheep, deer, pigs, camels, and hippopotamuses. They resemble the perissodactyls in habit and general shape, but they have achieved these in different ways. In particular, as the limbs lengthen they do so on an axis running between the third and fourth digits, so that the most highly developed forms, the camels, are unguligrade on the nails of these two only. The first digit is absent from all modern species, and the cattle and deer show various degrees of reduction of digits two and five. In all these, but not in the pigs, the third and fourth metapodials are fused to form a single cannon-bone (Figs. 25.15, 25.16). As in the horses, the limbs have pulley-like joints and there is no clavicle. The incisors tend to be reduced, and the cattle and sheep have none in the upper jaw; the canines may form fighting tusks, or may be small or absent, when they are often functionally replaced by horns or antlers, especially in the males. The cheek teeth generally have a complicated grinding surface, which tends to be selenodont, i.e. to have crescentic ridges, but those of pigs, which are omnivorous, are bunodont. All the higher forms, including the cattle and deer, have a complicated quadruple division of the stomach (Fig. 25.17) and chew the cud so that bacteria may assist in the digestion of cellulose. They thus achieve the same result as is got by the refection of rabbits (p. 442).

The wild boar (*Sus scrofa*) became extinct in Britain during the later Middle Ages, and the cattle and sheep are represented, apart from domestic breeds, only by a few herds of park cattle (*Bos taurus*) which possibly represent enclosed remnants of the former truly wild herds. They are white, with black or red ears. The two existing native British deer are the red (*Cervus elaphus*) and the roe (*Capreolus capreolus*). The former was for long

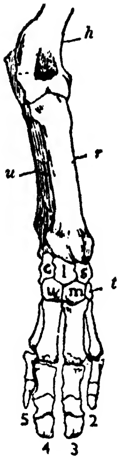


FIG. 25.14.—The bones of the foreleg of a pig.—From Thomson.

c., Cuneiform; *h.*, humerus; *l.*, lunar (semilunar or intermedium); *m.*, magnum; *r.*, radius; *s.*, scaphoid; *t.*, trapezoid; *u.*, unciform; 2–5, digits.

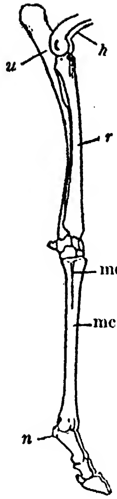


FIG. 25.15.—The bones of the right foreleg of a calf, from the outer side.—From Thomson.

h., End of humerus; *mc.*3.4, cannon bone (fused third and fourth metacarpals); *mc.*5, fifth metacarpal; *n.*, nodule; *r.*, radius; *u.*, olecranon process of ulna.

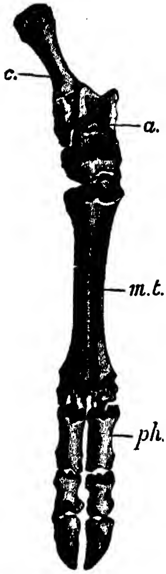


FIG. 25.16.—The bones of the hind foot of an ox.—From Thomson.

a., Astragalus; *c.*, calcaneum; *m.t.*, cannon bone (fused third and fourth metatarsals); *ph.*, phalanges.

confined to the Scottish Highlands, except for small herds in the New Forest and Westmorland, and rather more on Exmoor, but it is now present in some of the State Forests near these three

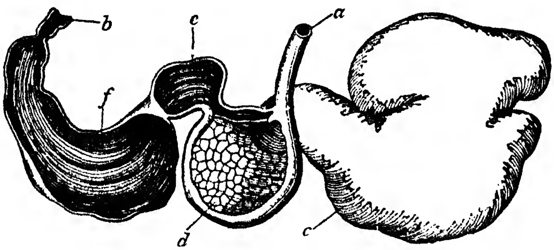


FIG. 25.17.—The stomach of a sheep.—From Leunis.

a., Oesophagus; *b.*, beginning of duodenum; *c.*, rumen or paunch; *d.*, reticulum in honeycomb; *e*, psalterium or manyplies; *f.*, abomasum or reed.

centres, which suggests that it has taken advantage of the increased area of relatively undisturbed woodland provided by the Forestry Commission. It is by nature an animal of the woods, and it is only necessity that has driven it to the hills of the west and north. The roe has also expanded its range and is now found in woodlands in various parts of England. The fallow deer (*Dama dama*), introduced centuries ago and commonly kept in parks, has also benefitted by the planting of the past thirty years, and is now more widely spread, as a truly wild animal, than either of the other two species. A few other introduced species of deer have also become wild in some woods.

MARSUPIALIA

Besides the eutherian mammals which suckle their young there are two other subclasses in existence in the world to-day.

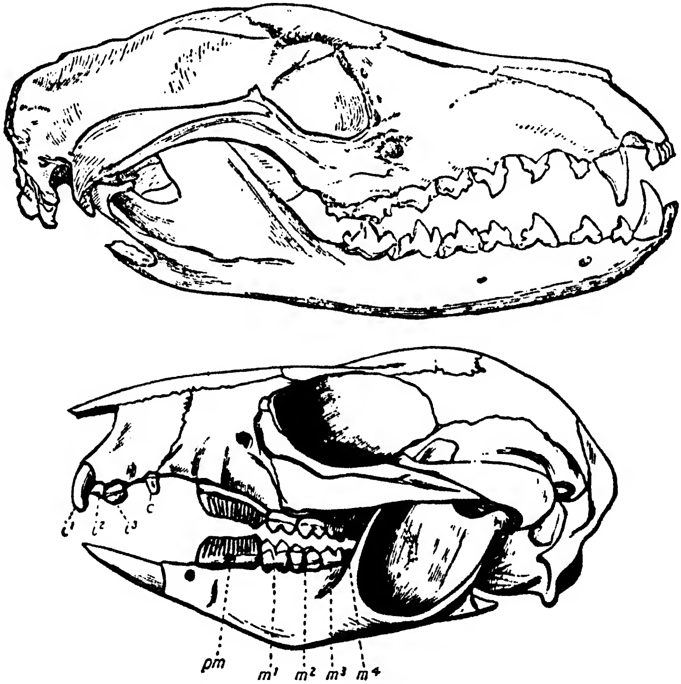


FIG. 25.18.—Skulls of a thylacine (above) and of a rat kangaroo (below).—From Young, *The Life of Vertebrates*, 1950. Clarendon Press, Oxford. After Flower and Lyddeker.

c., Canine ; *i.*, incisor ; *m.*, molar ; *pm.*, premolar.

The more advanced of these are the Metatheria or Marsupialia. The most striking feature is that the young, though born alive, is very small and climbs tropistically to the nipple and there becomes attached for a long time. The mammary glands are situated in an abdominal pouch or marsupium, supported by bones attached to the pubes, and milk is pumped into the baby, which has a forward prolongation of the larynx into the nasal passage (a true larval character, p. 244) so that it shall not choke. There is no true placenta. Apart from the method of care for the young, which is rather specialised, the marsupials have remained somewhat primitive. Their skull (Fig. 25.18) has many of the features found in insectivores, such as the fenestrated palate and the absence of a tympanic bulla, but can be distinguished by the fact that the angle of the lower jaw is turned inwards (' inflected ') to form a horizontal shelf (Fig. 25.19). The lacrimal

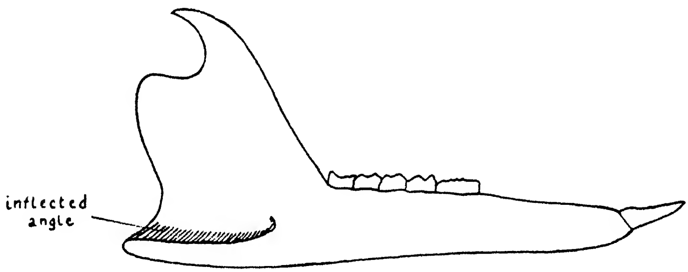


FIG. 25.19.—Dentary of kangaroo, inner surface, showing the inflected angle.

bone is exposed on the face, with its foramen on the edge of or outside the orbit, and the jugal takes part in the articulation of the jaw. There is a cloaca, and in most forms not only the uterus but the vaginæ of the two sides are separate, and to match these the penis, which hangs behind the scrotum, is bifid. The marsupials are now, except for a few American species, confined to Australasia, and there, away from the competition of the placentals, they have radiated in a number of directions which parallel many of the eutherian orders. Thus *Dasyurus* and *Thylacinus* are carnivorous and have dentition much like a dog's ; the kangaroos (*Macropus*) are herbivorous, with lophodont molars, and others are arboreal, rat-like and fossorial. There are no truly flying or aquatic marsupials, but *Chironectes* lives in rivers, and other genera

resemble the flying squirrels. Some marsupials have four or five incisors in each quarter of the jaw, and others are notable for ' syndactyly ', a condition in which the second and third digits of the hind-limb are small and bound together in a common sheath. In the opossums (*Didelphis*), which are arboreal, this appears to be because the hallux, which is opposed to digits four and five so that the foot can grasp a bough, has squeezed them nearly out of existence. The presence of syndactyly in ground forms like the kangaroos, which have no hallux, is held to suggest that they had arboreal ancestors.

MONOTREMATA

There remain the Prototheria or Monotremata, of which there are only two genera, *Echidna* (=*Tachyglossus*), the spiny ant-eater, and *Ornithorhynchus*, the duck-billed platypus (Fig. 25.20),

FIG. 25.20.—Duck-billed platypus (left) and Echidna. Drawn from photographs. From Young, *The Life of Vertebrates*, 1950. Clarendon Press, Oxford.

both confined to Australasia. They have the characteristic mammalian features of hair, diaphragm, and the rearrangement of the lower jaw bones, but they retain many reptilian features, such as separate pterygoids, postorbitals and prevomers, large clavicles and an interclavicle, and both coracoids and precoracoids (Fig. 25.21). They have no corpus callosum ; their temperature, although higher than that of their surroundings, is variable ; and they possess a cloaca. Above all, they lay large yolky eggs. After hatching, the young is nourished in a pouch by milk produced in specialised sweat glands. Both genera are specialised,

Echidna with its spines and ant-eating habits, and the platypus for aquatic life. Neither has teeth.

Neither marsupials nor monotremes can be looked on as ancestral mammals, and fossils give us little indication of their connection with the placental stock. A reduction in the lower jaw can be traced in a number of fossil reptiles of the group Synapsida, and from these we may assume the mammals to have come. There are other extinct groups which have only the dentary in the lower jaw, and so are classed as mammals, but we have no means of telling if they had hair and warm blood or how they fed their young, so that we cannot tell when mammals, as we know them to-day, originated. Unless milk, hair and temperature control arose together three times over, the three modern groups must all be descended from the first mammals, but they early diverged. The marsupials show signs of having lost a placenta, and so perhaps they left the eutherian line soon after it was established, but the monotremes have a remoter connection with the other two. If we wish to have a mental picture of a prototypical mammal we must think of a creature which combines the teeth, habits and general build of an insectivore with the egg-laying and other reptilian features of the platypus. Such a creature perhaps lived a hundred million years ago at the end of the Jurassic period.

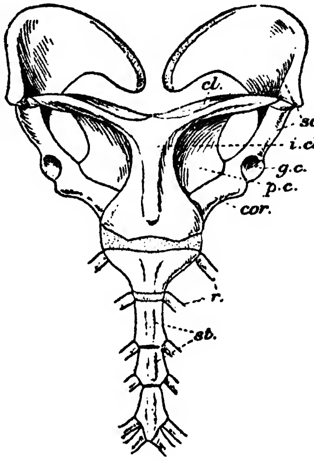


FIG. 25.21. — The shoulder girdle and breastbone of a duck-mole.

cl., Clavicle ; *cor.*, coracoid ; *g.c.*, glenoid cavity ; *i.cl.*, interclavicle ; *p.c.*, precoracoid ; *r.*, ribs ; *sc.*, scapula ; *st.*, sternebræ.

26

THE CELL AND MAMMALIAN HISTOLOGY

We have from time to time in this book used the word 'cell', but have not defined it; nor shall we attempt now a formal definition which would satisfy a philosopher, for the concept of which it is the name is one of those, common in biology, where the general meaning is clear but the limits impossible to lay down.

When an animal is closly examined there is an obvious distinction between parts which are living and those which are not; the sentence, 'I have cut my finger to the quick', where 'quick' is used in the Biblical sense of 'alive', shows that long before zoology was a science the popular mind made a distinction between the living part of the body and the dead or formed parts such as hair or nails or the outermost layers of the skin. More detailed investigations confirm this distinction, and to the material of which the living parts of the body are made the name protoplasm is applied. This term had previously been proposed in 1848 by Hugo von Mohl for the living part of the plant cell—that portion which lies between the watery sap and the wall. It is now used generally for all the living material of both plants and animals. Microscopic investigation shows that most often this protoplasm is not in one continuous mass, but is separated into a number of separate units by some sort of wall. These units are called cells, and the simplest definition of a cell is 'a quantity of protoplasm surrounded by some sort of wall'. The word 'cell' means a small room, and in prisons it still has that sense. It was used by Robert Hooke in 1665 for the small cavities and their walls which can be seen in cork, and which are in fact dead plant cells, and from that starting-point its meaning has slowly changed. It was early known that many cells contain a specially dark part, and Robert Brown in the early part of the nineteenth century recognised that this was a normal feature of plant cells and called it the nucleus, although he did not invent this use of the word. We now generally deny the name cell to anything which does not contain a nucleus, and define a cell as 'a quantity of protoplasm containing a nucleus and surrounded by some sort of wall'. There are,

as we shall see later, many inconsistencies in our use of the term, for it is sometimes applied to things with two nuclei or none. A mass of protoplasm including two or more nuclei within one wall is more strictly called a cœnocyte, where it is the whole body of an animal, or a syncytium where it is a part of the body. We have seen examples of the former in Protozoa such as *Paramecium* and some *Amœbæ*, and shall meet the latter in tissues such as muscle.

CYTOPLASM

It is often convenient to distinguish the material of which the nucleus is composed as nucleoplasm and the rest of the cell as cytoplasm.

Detailed investigation of the chemical nature of cytoplasm can only be carried out by killing it, and we can be reasonably confident that at death chemical changes occur, but there are unlikely to be large transformations of one type of chemical substance into another. Work on dead cytoplasm can therefore give us useful information, and in addition a limited number of experiments can be done without causing death. Most of the cytoplasm is water, and in this are present, in true or colloid solution, several other substances; the most important are the proteins, which make up about sixty per cent. of the dry weight, and others are carbohydrates, fatty substances or lipoids, and inorganic salts and ions—the same things, in fact, as are needed in the diet. Some other organic substances are present in small quantities. In the cytoplasm are what are called inclusions of two sorts; some are protoplasmic, that is, are themselves living and are chemically distinct specialisations of the cytoplasm, and others, called deutoplasmic, consist of non-living material formed by the cell. The chief of the protoplasmic inclusions will be referred to below. The deutoplasmic inclusions are granules, crystals or globules of substances present in too great a quantity to be held in solution; the most obvious are the yolk granules of egg cells, fat globules, and particles of pigment in many cells.

The nineteenth-century workers all thought that cytoplasm had a structure of visible fibres or surfaces, so that it was described as a network or as a foam, but in fact these are the appearances of dead cytoplasm induced by the action of the fixatives; a solution of protein, such as white of egg, when treated in the same

way shows the same structure, although it previously had none. The obvious ability of cytoplasm to flow, as in *Amœba* or in many plant cells, shows that it is a liquid, and many determinations of its viscosity (that is, its internal friction, or resistance to flow) show this to be only a little greater than that of water. At times, however, some cytoplasm is much stiffer, and must be accounted as solid, as in the outer part of an *Amœba*. The simple explanation is that all cytoplasm is a colloidal solution,

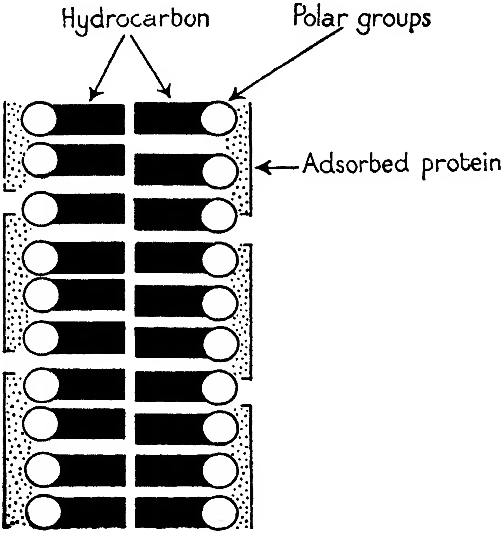


FIG. 26.1.—Diagram of molecular structure of the plasma membrane.—From Danielli. Bourne, *Cytology and Cell Physiology*, 2nd edition, 1951. Clarendon Press, Oxford.

comparable to that of gelatine and water ; usually water is the continuous phase, and the material is liquid and flows, but at times the proteins make the continuous phase and the material gelates and is solid. Reversible changes of phase are easily induced in gelatine/water solutions by changes of temperature or acidity, and it is easy to imagine these having similar effects in the cell. Cellular death induces—or perhaps is caused by—irreversible changes, such as that which occurs when an egg is boiled. If there were not some sort of wall or membrane at the cell surface there would be nothing to prevent the aqueous cytoplasm mixing with any water with which it came into contact. It does not do

so, and all cells appear to have a surface in which the protoplasm is differentiated so as not to mix with water. This wall produces a slight tension, about one two-hundredth of that at an oil/water interface, which is usually called the surface tension of the cell. Some substances penetrate the wall easily, others more slowly or not at all, and since some of those which go through are water-soluble and others are fat-soluble, it has been suggested that the cell membrane is a mosaic of lipoids and proteins (Fig. 26.1). In addition to the protoplasmic wall there may also be a gelated layer, or a dead secreted layer such as the keratin of the skin.

The normal hydrogen ion concentration of the cytoplasm appears to be slightly on the acid side.

THE FINE STRUCTURE OF CELLS

During the past decade our knowledge of the fine structure of cells has been greatly increased by the use of the electron microscope, which has raised useful magnifications from about 2000 to 100,000 or more. Cells cannot be *seen* under the electron microscope, and the cytoplasm has to be killed and is often loaded with particles of a heavy metal such as gold in order to provide what are, in effect, silhouettes, so that caution must be used in interpreting electron micrographs, but some points seem clearly established.

The most important is the widespread occurrence of double membranes, two layers which are opaque to the electron beam separated by a less opaque layer. The cell surface is of this nature, and is usually about 120 Å thick. Since the two layers take up osmium tetroxide they are presumably fatty in nature, and there is thus support for the theoretical model shown in Fig. 26.1.

The electron microscope shows no structure for the matrix of the cell, that is for cytoplasm in general, but it does show that membranes are much more widely distributed than was formerly thought.

CYTOPLASMIC INCLUSIONS

Mitochondria are filaments, granules, or spheres which are generally scattered through the cytoplasm and are sometimes visible in the living cell (Fig. 26.2). A common length is about

4 μ, and there may be from 50 to 5,000 in a cell, the highest numbers being found in cells such as those of liver that are metabolically active. Each has a wall which is a double membrane; in the gland cells that have been most clearly examined it extends into the hollow of the mitochondrion to make complete or incomplete partitions, so that it is similar to a mitochondrion in *Amœba* (Fig. 2.3). Mitochondria can be centrifuged out of crushed cells in large numbers, and their chemical activity investigated. They carry out the energy-providing reactions of the cell, and the carbohydrate-splitting enzymes of the tricarboxylic acid cycle (p. 536) seem to be situated in their interior, the oxidative enzymes for the reactions with cytochrome in which alone molecular oxygen is used, in their walls.

Lysosomes are bodies of similar size to mitochondria but without the internal partitions. They contain the enzymes that hydrolyse large molecules of fats, proteins and nucleoproteins.

Near the nucleus, or distributed through the cell, is a much larger inclusion, called the endoplasmic reticulum. It consists of a much-folded double membrane (perhaps not, in spite of its name, a net), which in micrographs appears to be connected with the surface, so that its double membrane is continuous with that of the cell wall. It is studded with ribosomes, particles of ribonucleic acid, the function of which is discussed below (p. 504).

A similar folded membrane without ribosomes has been called the Golgi body. This was first described in 1898, but as hardly any two microscopists have applied the name to the same structure and its function is unknown, the elementary student need not trouble himself with it. The kinetoplast of flagellates (p. 64) has a similar structure of a pile of double membranes without ribosomes.

The centrosome is a small body, not yet found in plant cells, which is in the cytoplasm but is important in nuclear division (p. 696). In section it is seen to include a ring of 9 rods, and thus has a close similarity to a flagellum (p. 40). In the Protozoa, the basal granules of flagella, which have a similar structure, often act in the same way in controlling the division of the nucleus. Centrosomes normally occur in pairs, the axes of the rods of the pair being perpendicular to each other.

NUCLEOPLASM

Nucleoplasm is physically similar to cytoplasm. It is aqueous, with a viscosity rather greater than that of water, it gelates when damaged, and it is separated from the cytoplasm by a membrane comparable to the cell membrane. Chemically it is rather simpler, with a high proportion of protein and much phosphorus, but lacking many elements which are present in cytoplasm. Numerous experiments have shown that although cells can live without their nuclei, their activities are much restricted ; roughly speaking, the cell can carry out catabolic processes but not anabolic. The special importance of the nucleus in transmitting the hereditary characters is discussed in Chapter 29.

The nuclear membrane is of the normal double form, though in some micrographs there appear to be gaps in the outer layer. A darkly-staining body, the nucleolus, is rich in ribonucleic acid, but its function is unknown. The chromosomes, clearly visible only when the cell is dividing, consist of an axis of deoxyribonucleic acid which is coiled into a double helix like that of a coiled-coil electric light bulb. After division the chromosomes lengthen, untwist, and finally disappear, but their importance has led to the assumption that they remain in existence though invisible. In growing eggs they persist in an untwisted elongated form with many lateral loops projecting from the axis. This condition is generally called ' lamp-brush ' but in England, where oil lamps have been almost entirely replaced by the electric light, ' bottle-brush ' would be a better description. The axis of a loop is of deoxyribonucleic acid, but it is surrounded by a film of ribonucleic acid. Each loop starts from a thickened part of the main axis that is apparently still spiral, and is characteristic of its position on a particular chromosome.

THE SYNTHESIS OF PROTEIN

The nucleic acids, usually associated with proteins as nucleoproteins, are important constituents of the cell. There are many different kinds of them, but each consists of from 15 to several thousand nucleotides, each of which is made up of phosphoric acid, a pentose carbohydrate, and four nitrogenous bases. Usually there are some thousands of nucleotides, and the molecular

weight is of the order of millions. In deoxyribonucleic acid (or desoxyribose nucleic acid, DNA for short) the sugar is mostly *d*-2-deoxyribose and the bases adenine, thymine, guanine and cytosine, while in ribonucleic acid (or ribose nucleic acid, RNA for short) the sugar is almost exclusively *d*-ribose and in place of thymine there is uracil. The carbohydrate groups are linked in a long chain through the phosphates, and the bases make side chains. The protein in a nucleoprotein makes a coat round the nucleic acid. The carbohydrate chain of deoxyribonucleic acid is double, each strand being wound into a helix and the two being intertwined and linked through their bases, which are joined by hydrogen bonds, adenine to thymine and guanine to cytosine. The numbers of adenine and thymine groups are always equal to each other, as are those of guanine and cytosine, but the proportion of adenine (or thymine) to guanine (or cytosine) varies, being however constant within a species. As the order of the bases can be varied indefinitely the number of possible isomers for a given chain length can be very large. The chain of ribonucleic acid is a single helix.

It seems that this arrangement of the bases, which may be likened to a long word spelt in four letters only, is the essential key to synthesis. Deoxyribonucleic acid is found almost exclusively in the nucleus, and in the growing cell it is synthesised. It seems that the two strands of an existing molecule separate, and that radicles available in the nucleoplasm arrange themselves alongside each half to form an image of it. Adenine comes opposite thymine and guanine opposite cytosine, and vice versa, so that when cross-linkages are formed the original double helix is restored, but there are now two molecules where formerly there was only one. In a similar way deoxyribose nucleic acid probably organises the formation of molecules of ‘ messenger ribonucleic acid ’ ; though uracil now pairs with adenine the pattern is preserved. These pass out into the cytoplasm, and in some way determine the composition of the ribonucleic acid of the ribosomes. On these the proteins are synthesised. Apparently each has a specific ribonucleic acid corresponding to it, so that the four-letter alphabet of the nucleic acid must somehow be translated into the twenty-letter alphabet of the protein, for there are some 20 amino acids, the sequence of which determines the identity of the protein molecule. Some part in this translation is apparently taken by short-chain soluble or transfer ribonucleic acids, each

of which is perhaps able to combine only with a single amino acid, and so carry it to the ribosome.

All these syntheses require energy, which is supplied by the hydrolysis of adenosine triphosphate, the reaction that supplies the energy for the contraction of muscle and other cells.

FIG. 26.2.—Drawing by Dr. H. B. Fell of a living fibroblast under dark-ground illumination. The nuclear membrane, two nucleoli, filamentous mitochondria, and fat globules are shown. × *c.* 1,000.—From Le Gros Clark, *The Tissues of the Body*, 3rd edition, 1952. Clarendon Press, Oxford.

CILIA AND FLAGELLA

As we have seen in the chapters on the Protozoa, these animals have many specialisations of the cytoplasm, such as pseudopodia, cilia, myonemes and axial fibres. Metazoan cells, as fits their greater specialisation, have fewer of these, although, as is described below, individual cells may have one specialisation,

especially pseudopodia or cilia, strongly developed. Cilia and flagella are especially interesting, because it appears from studies made with the electron microscope that those of green Algæ, of *Paramecium*, of *Hydra*, of molluscs, of the frog and of man, and sperm tails of many phyla, all have the same structure. Within a sheath there are two central strands, and a ring of nine surrounding them, making eleven in all. Each outer strand is sometimes split and their arrangement may be asymmetrical (Fig. 3.7). The outer strands continue into the basal granule, but the inner pair do not.

TISSUES

The resemblance of some parts of the body to a woven cloth led M. F. X. Bichart, at the beginning of the nineteenth century, to apply to them the French word *tissu*, of which the English form is tissue ; the name stuck, and a tissue may be defined, to continue the weaving metaphor, as any part of the body with a recognisable texture. The study of the tissues is called histology, from a Greek word meaning cloth. It has been chiefly developed for mammals, because of its medical importance, and the rest of this chapter is concerned primarily with them. Much of the descriptive matter, however, applies to other vertebrates, and the general principles probably apply to all Metazoa.

CELL TYPES

The traditional classification of tissues is based on their appearance, but in recent years a more logical division, founded on the type of cell of which they are chiefly composed, has become possible. In the second decade of this century it was discovered that most cells and tissues could be kept alive, away from the body which formed them, provided that they were given a supply of oxygen and organic food, which is usually derived from blood serum. Such cells are said to be growing *in vitro*, i.e. in glass vessels, instead of *in vivo*, in the living body, and the technique of dealing with them is called tissue culture. Some of the original cultures, made from chicks, are still alive, having outlived many generations of their species. Under some conditions of growth tissues *in vitro* maintain their original form, but under others they

undergo a process of dedifferentiation, in which the cells continue to grow but do not form organised structures. To some extent they change their form, and cells from different parts of the body come to resemble each other more closely, but it is this which helps us in classification. All cells in tissue culture belong to one or other of three (or perhaps four) main types, called the epitheliocyte, the mechanocyte and the amœbocyte (Fig. 26.3)

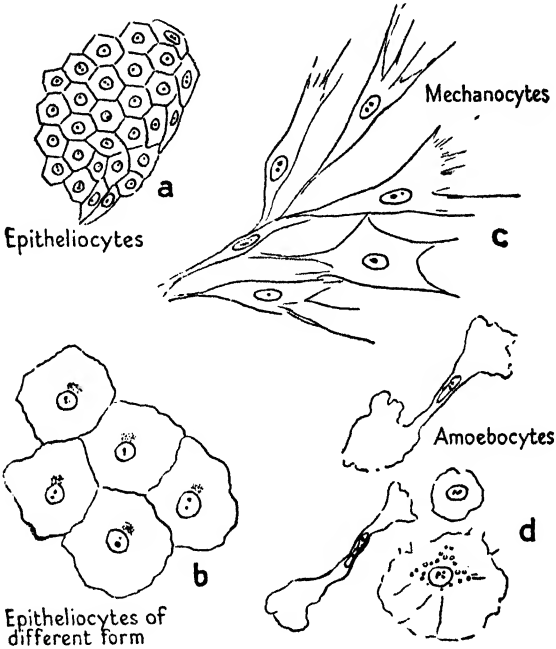


FIG. 26.3.—The primary groups of cells as seen in tissue cultures. The epitheliocytes in *b* are probably secondarily derived from mechanocytes.—From Willmer. Bourne, *Cytology and Cell Physiology*, 2nd edition, 1951. Clarendon Press, Oxford.

These are not only distinct morphologically, but also behave differently, and it is very doubtful whether one can ever change into another. Epitheliocytes are flattened, and their most characteristic property is that they stick to each other or to anything else, such as a glass surface, so that they form sheets or membranes and are rarely seen alone. When their growth is slowed down they often produce the protein keratin. Mechanocytes (often called fibroblasts, although this word is best used in a more restricted sense) are elongated and are capable of a mysterious type of gliding

movement, but they usually form a three-dimensional network. Amœbocytes are, as their name implies, amœboid in form; they remain isolated from one another, and move relatively rapidly by the formation of blunt pseudopodia, which are also used for ingesting foreign particles. The three types of cell differ also in their nutritive requirements; epitheliocytes are especially dependent on an adequate glucose concentration in the medium, mechanocytes on unknown substances present in extract of embryos, while amœbocytes are the least exacting.

The fourth possible primary type is the nerve cell, which is difficult to fit into any of the other three classes, having some resemblance to all of them. The same is true of the cells of the neural crest (p. 654), but as these develop variously into such mechanocytes as cartilage cells and such amœbocytes as the dendritic cells of the skin, they are perhaps best looked on as undifferentiated embryonic cells.

CLASSIFICATION OF TISSUES

Most tissues contain more than one type of cell, but almost every tissue is made chiefly of one of the three main types that we have described, and on this fact may be based a classification of the tissues which is more rational than the traditional one. Epithelium is tissue which is made predominantly of epitheliocytes; it corresponds closely to epithelium defined in the old way as tissue in which there is little ground substance, that is, material formed outside the cells by the cells. Nervous tissue may be looked on either as a subdivision or as a derivative of epithelium; it comes from epithelium in development, but its characteristic cell, the neurocyte, is different in appearance and properties from the epitheliocyte, and will not divide when grown in tissue culture. Mechanical tissue is based on the mechanocyte; it includes connective tissue, muscle, and the skeletal tissues, cartilage and bone. Tissue based on amœbocytes has no obvious and simple name, but may be called amœboid tissue if it is remembered that it is not the tissue itself but its cellular constituents which are amœboid. It corresponds roughly to what are also called the fluids of the body. These three (or four) tissues and their subdivisions will now be further described.

EPITHELIA

As has already been said, epithelia are characterised by having little ground substance, so that the cells are in close contact; microdissection has shown that they stick together by their protoplasmic borders, and in some stained preparations intercellular protoplasmic threads can be seen running from one cell to the next. There is usually one, occasionally two, nuclei per cell. Epithelia generally form the surfaces of the body. They are usually classified by the shape of the cells and the number of

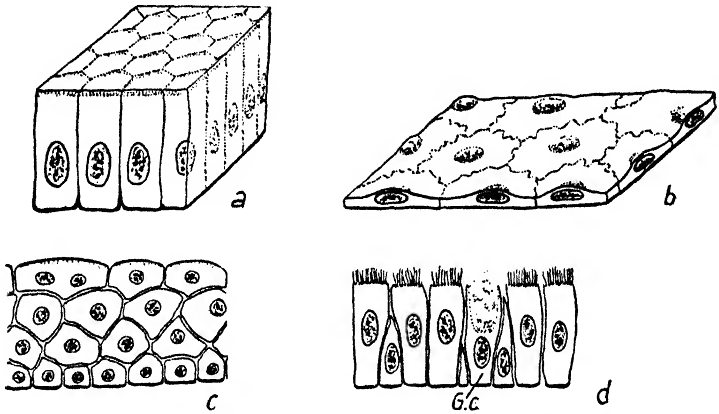


FIG. 26.4.—Diagrams of epithelia.—From Le Gros Clark, *The Tissues of the Body*, 3rd edition, 1952. Clarendon Press, Oxford.

a., Simple columnar; *b.*, pavement; *c.*, transitional; *d.*, ciliated columnar, showing a mucus-secreting goblet cell (*G.c.*).

layers, but although the names used must be known for descriptive purposes this type of classification is not of fundamental importance. The epithelia of different parts of the body are specialised for different purposes, and experiments have shown that even the epithelium of a given part of the external surface, such as the flank, the sole of the foot, the cornea or a claw, retains its specific appearance when grafted into another position. The best classification of epithelia will therefore be made by considering their position and function, and the extent to which they maintain their identity.

If the cells make a single layer the epithelium is said to be simple. According to the shape of the cells it is called pavement or squamous (where they are flattened), columnar, cubical, or

polyhedral, but there are intermediate shapes. Columnar and cubical epithelia may have cilia on their free surfaces, when they are called ciliated, and columnar, cubical and polyhedral epithelia may be glandular, passing secretions through their walls. Pavement or columnar and polyhedral epithelia may be associated together to form three or four layers, giving transitional epithelium, or several layers, when the result is stratified epithelium. The outer layers of this are usually keratinised, and the cells dead. Some of these types of epithelium are shown in Fig. 26.4. They may be summed up in the schema :

$$\text{Simple } \textit{or} \left\{\begin{array}{c}\text{transitional}\\ \textit{or}\\ \text{stratified}\end{array}\right. \left\{\begin{array}{l}\left.\begin{array}{l}\text{cubical}\\ \text{columnar}\end{array}\right\}\text{ ciliated } \textit{or}\\ \text{polyhedral}\\ \text{pavement}\end{array}\right\}\text{ glandular}$$

Examples of some functional types of epithelia will now be described.

THE EPIDERMIS

The skin is much more than a mere epithelium, but its outer part, the epidermis, is a good example of a stratified epithelium (Figs. 22.3, 26.5). The inner layers, called collectively the stratum of Malpighi, have cells which range from roughly columnar in the deepest part to a flattened polyhedral form above. The nuclei are conspicuous and actively mitotic, and as the cells divide they push the older cells outward ; this accounts for the gradual flattening as the surface is approached. There are no blood vessels, but there are intercellular spaces which may allow the diffusion of foodstuffs, and the cells are connected by protoplasmic threads. Outside the stratum of Malpighi is the stratum granulosum, of two or three layers, and then the stratum lucidum. These appear in stained sections, as their names imply, as respectively full of granules and clear. They are stages in the death of the cells ; mitosis (p. 696) has ceased, the nuclei become progressively less distinct, and the formation of keratin has begun. The stratum corneum which is on the surface consists almost entirely of keratin; cells cannot be recognised, and there is no living protoplasm. It may be thicker than all the other layers together. Its outer surface is worn away by friction or falls off in thin flakes, and it is continually renewed from below. We have seen above (p. 509)

that there are different types of epidermis and that these maintain their nature after transplantation to another part of the body. Two of the most striking are those of the sole of the foot, where the stratum corneum is extremely thick and the mitotic activity of the Malpighian stratum great, and the cornea, where the cells are completely transparent and there is no flaking from the surface.

A similar stratified epithelium lines the mouth, and keratinised cells for examination under the microscope can always be

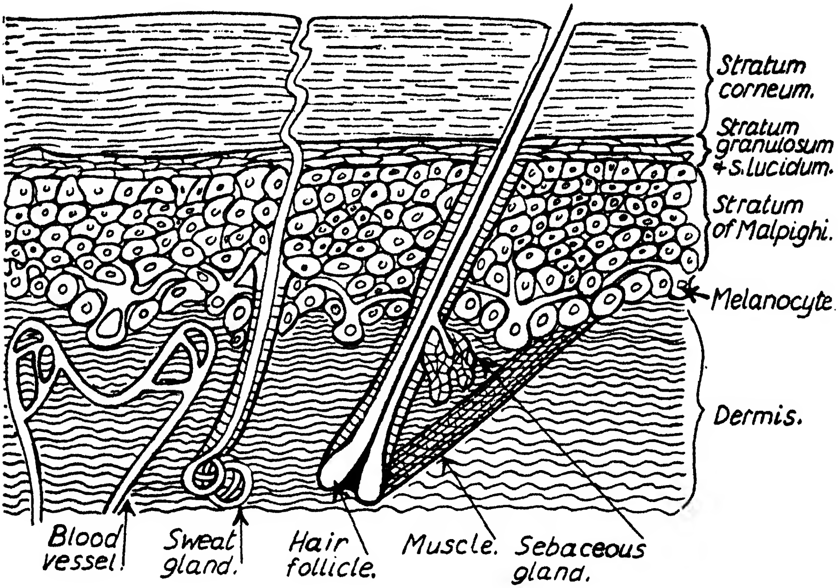


FIG. 26.5.—A diagrammatic transverse section of mammalian skin.

obtained by scraping the inside of the cheek with the handle of a scalpel. At places in the mouth of a young mammal (and on the surface of the body in cartilaginous fishes) the cells of the epithelium become specialised and sink in to become ameloblasts, which produce the enamel which makes the outer layer of teeth and placoid scales. It contains a little organic matter, including some keratin, but 99·5 per cent. of it is inorganic, probably mostly calcium hydroxyapatite, with traces of iron and copper. It is as hard as sapphire.

Another type of stratified epithelium lines the trachea and bronchi. Several layers of closely packed cells have on their outer layer a columnar layer which is ciliated (Fig. 26.4).

Transitional epithelium is found only in the urinary passages, such as the ureter, bladder, and urethra. The inner cells are not closely packed, so that they can slip over one another and the membrane is easily stretched; this is especially important in the bladder. The surface cells are somewhat flattened, and often have two nuclei each ; there is a thin cuticle (Fig. 26.4).

GLANDS

A good example of a simple columnar epithelium is that which lines the intestine. There is a single layer of cells, roughly hexagonal in cross section, and with a height about two and a half times their diameter (Fig. 26.7). Many of the cells are glandular

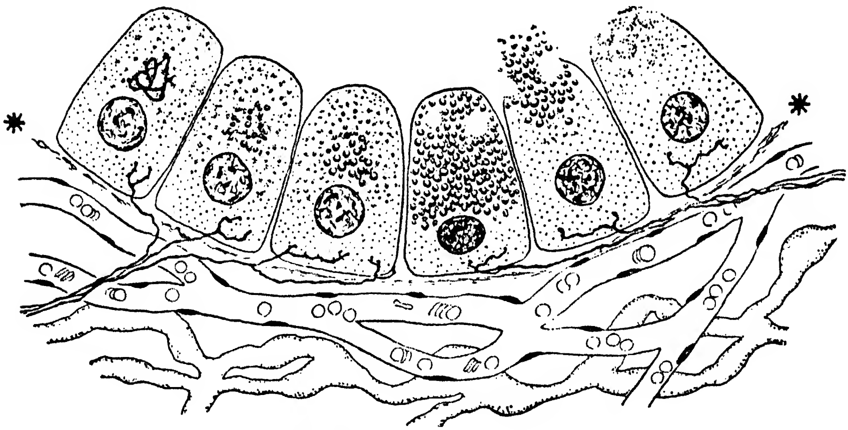


FIG. 26.6.—Diagram to illustrate the cycle of activity in a secretory cell. Efferent nerve fibres, blood capillaries, and (on a deeper plane) a lymphatic plexus are shown. * *, basement membrane. The cell on the extreme left shows the Golgi apparatus ; secretory granules appear around this, some of them become liquefied, and (on the right) they are discharged from the cell.—From Le Gros Clark, *The Tissues of the Body*, 3rd edition, 1952. Clarendon Press, Oxford.

in function, and perhaps all become glandular in turn. Especially conspicuous are the goblet cells, so called from their shape, which secrete mucus. Both from these and from the enzyme-producing zymogen cells the secretion is liberated at the free border of the cell. In some other glands, such as those which produce milk in the breast, the border partially breaks down. In both types the cell goes through repeated cycles of activity, so that although the discharge of a secretion by a gland may be continuous, that by each individual cell is intermittent (Fig. 26.6). In the sebaceous

glands of the skin the whole cell disintegrates in order to liberate its secretion. Although glandular epithelium generally remains a single layer it often becomes invaginated from the surface so that, in association with connective tissue, blood vessels and so on, it forms a gland. According to the type of branching and extent of the secretory surface various names are given to glands; some are shown in Fig. 26.7. Many of the endocrine glands, which produce hormones (pp. 469–71), begin as ordinary epithelial glands with ducts; when they lose these the cells discharge their products either into small intercellular spaces or into relatively large vesicles, and from both of these the secretion passes to the blood stream. The islets of Langerhans consist of solid masses of cells which have lost much of their epithelial appearance while retaining its character, and the thyroid has vesicles surrounded by a single layer of cubical cells with conspicuous nuclei. Other endocrine glands, such as the posterior pituitary and adrenal medulla which are derived from nervous tissue, and the interstitial cells of the gonads which are mesodermal in origin, are not epithelial.

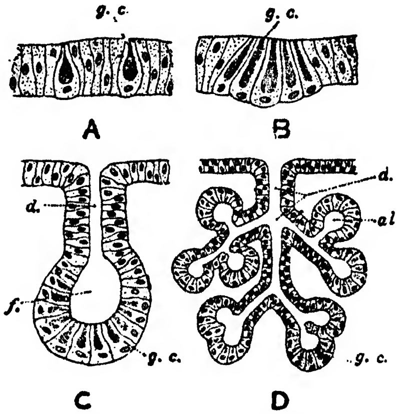


FIG. 26.7.—Diagrams of different kinds of glands.—Partly after Lang.

A, Columnar epithelium containing isolated gland cells or *unicellular glands*. *B*, similar epithelium with the gland cells collected into a group so as to form a *flat multicellular gland*. *C*, a *hollow multicellular gland* of the *simple* kind. *D*, the *compound or racemose glands*.

al., Alveoli or acini of the racemose gland; *d.*, ducts; *f.*, alveolus or fundus of simple gland; *g.c.*, gland cells.

Non-glandular simple epithelium is found in the lungs and in various ducts. In the terminal bronchioles, the final air-tubes which lead into the lungs, it is cubical, while in the alveoli or small blind chambers which make up the mass of the lung itself it is pavement. A simple columnar ciliated epithelium lines the bronchi.

The part of the cœlomic wall which gives rise to the germ cells is often called germinal epithelium, but if 'epithelium' is considered, as it should be, as a name for a specialised tissue made from specialised cells, it is not appropriate to a part of the body consisting of totipotent cells, that is, cells which can

develop into a complete organism and give rise by mitosis to epitheliocytes, mechanocytes, and amœbocytes in all their variety. Sensory epithelium, which is best regarded as a specialisation of nervous tissue, is mentioned below (p. 540).

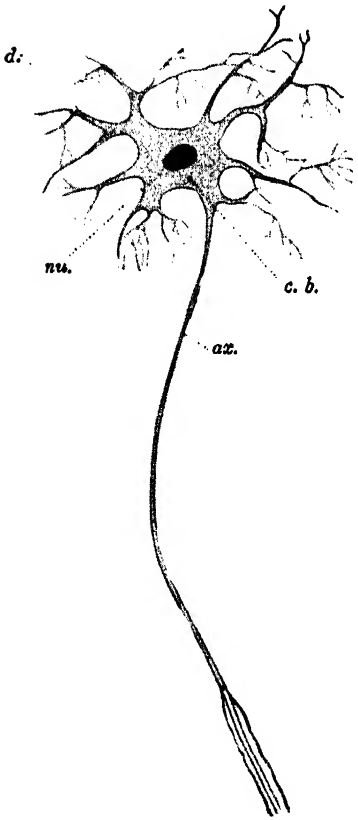


FIG. 26.8.—Diagram of part of a neuron highly magnified.
ax., Axon; *c.b.*, cell body; *d.*, dendrites; *nu.*, nucleus.

NERVOUS TISSUE

Nervous tissue is derived from an undifferentiated epithelium of the embryo, but its cells are so different from all others that it is best treated on its own. The typical nerve cell or neuron (Fig. 26.8) is large—of the order of 100 μ in diameter—with a conspicuous nucleus and a number of branched processes called dendrons or dendrites. There is also usually another process, much longer and seldom branched except at its extreme end, called an axon. The dendrons, and often the branched ends, called terminal arborisations or telodendria, of the axons, come into close contact with dendrons or the cell body of other neurons. The central nervous system consists mainly of masses of such cells making a solid network (Fig. 26.26). There are also non-nervous packing cells called collectively neuroglia; they are derived from the same embryonic epithelium as the nerve cells. They occupy all the space between the nerve cells, so that they make an internal connective tissue. There is much evidence, both anatomical and functional, that there is no protoplasmic continuity at the point, called a synapse, where one neuron makes contact with another.

NERVE FIBRES

Many axons leave the central nervous system and each in doing so becomes the centre or axis cylinder of a nerve fibre. The other parts of this are shown in Fig. 26.9. The endoneurium is collagenous and so presumably formed by connective tissue cells (see p. 517). The Schwann cells, like the neuroglia, are derived from the same embryonic epithelium as the nerve cells. It is possible, and theoretically probable, that the Schwann cytoplasm extends over the whole length of the fibre, but if so it is very thin. The myelin or medullary sheath is a layer of fatty material which is not present in young or small fibres, and it is the blackening of the fat which gives the characteristic appearance to osmium tetroxide preparations of nerves. At intervals the sheath is broken and the axon is visible ; these breaks are called nodes of Ranvier. The fact that there is one Schwann nucleus in each internode, and other evidence, suggests that the Schwann cells control the deposition of the myelin. Careful staining shows that the axon has many longitudinally-running neurofibrils, which are also visible in the bodies of nerve cells. The electron microscope shows that an axon contains little but fibrils of about 100 Å in diameter, each of which may be a single molecule of a fibrous protein. Dendrites have fibres of twice the diameter, and protoplasm containing an endoplasmic reticulum. From the Protozoa upwards, cytoplasm which is concerned in conduction tends to have a fibrillar structure. Nervous impulses may be carried in any direction in the cells, but the synapses have one-way conduction only, so that in life there is directed flow through the nervous system. The electron microscope shows a greater density of granules and mitochondria on the presynaptic side. In some sense organs, such as the eye and nose (p. 510), nerve cells are arranged in plates of tissue which simulates an epithelium, and is often referred to by that name.

MECHANICAL TISSUE

Mechanical tissues may contain amœbocytes as well as the mechanocytes which are their fundamental constituents, but their chief structural property is that they contain much intercellular or ground substance, formed by, but external to, the cells

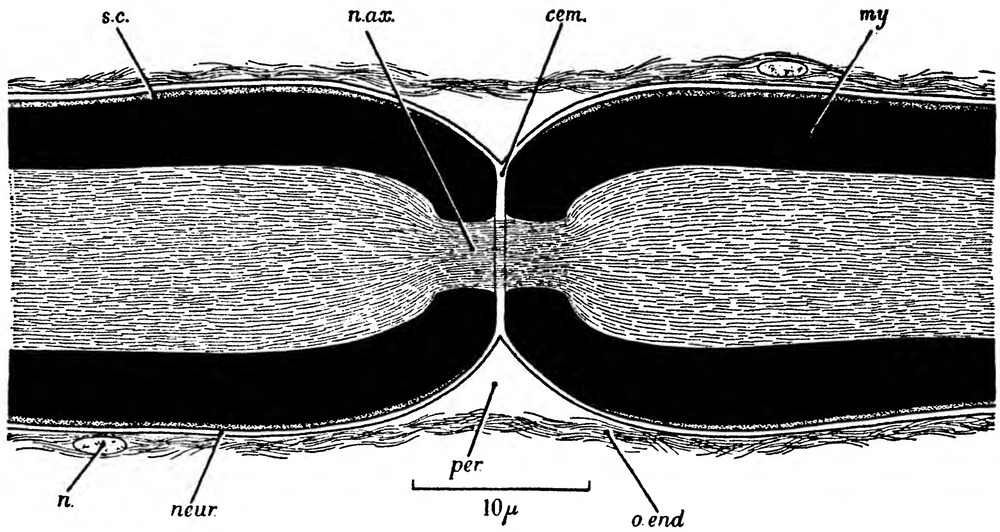


FIG. 26.9.—A diagram of a nerve fibre at a node of Ranvier.—From Hess and Young, *Proc. roy. Soc. B*, 1952, **140**, 301.

cem., Cementing disc; *my*, myelin; *n.*, nucleus of outer endoneurium; *n.ax.*, nodal axon; *neur.*, neurilemma; *o.end.*, outer endoneurium; *per.*, perinodal space; *s.c.*, protoplasm of Schwann cell.

themselves. It may be in the form of fibres or plates, or may be simply a homogeneous jelly or fluid, but whatever its form, it is not itself living. Although the best classification of mechanical tissues would be by the types of cell, for it is on these that the ground substance depends, it is convenient in practice to work from the whole appearance of the tissues. This depends in great part on the intercellular substance, and as this is also intimately related to the function of the tissue, a classification so derived is physiological as well as morphological.

CONNECTIVE TISSUE

The least specialised of mechanical tissues are the connective tissues, the chief feature of which is the fibre. They serve not only to connect one organ or tissue with another, but also, especially where in their more highly developed form they make tough sheets or fasciæ, to separate them. The ordinary process of dissection of blood vessels and nerves consists in cutting and tearing connective tissue, and it is only in the first opening of the body and in some special circumstances that anything else should ever be cut. The simplest connective tissue is areolar, which is well seen in the white meshwork which in most places joins the skin to the underlying body-wall (Fig. 26.10). There is a more or less continuous jelly-like ground substance, which contains much chloride and so stains black with silver nitrate, and in this run branching and anastomosing bundles of white fibres. The material of which these are made is the protein collagen, which on boiling forms gelatin or glue (the difference between these two lies solely in their degree of purity). They may be recognised in a preparation by the facts that they show a wavy outline, and if broken do not pull the cut ends apart, and because although the bundles branch and meet again to form a network, individual fibres never do. In areolar tissue there may also be a few yellow or elastic fibres, which are made of another protein, called elastin and containing bound fatty acid, which is not hydrolysed by boiling. The fibres run singly instead of in bundles, and individual fibres branch and join each other; when one is cut its ends are pulled apart, showing that the fibre was under tension. There are also some other fibres, of which little is known, which appear to consist of a carbohydrate resembling cellulose. The chief cells

of areolar tissue are the fibroblasts, or fibrocytes, in the restricted sense, which spin outside themselves masses of cytoplasm

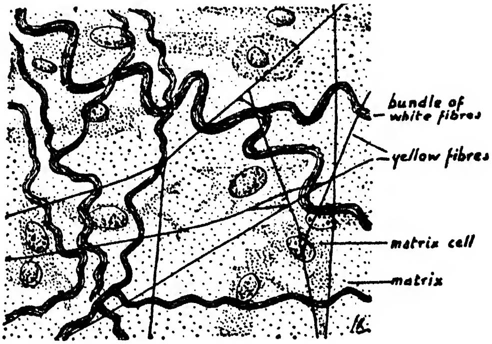


FIG. 26.10.—Fibrous connective tissue, areolar, from subcutaneous tissue of rabbit. × 300.—From Thomson.

which develops into the white fibres. The direction of the fibres is to some extent determined by any tension in the ground substance, so that on the whole they are formed in the way most useful to resist the stresses to which the tissue is exposed. This is the immediate explanation of why connective tissue is functionally adapted to its purpose. Fibrocytes are flattened, with two or three pointed processes, and are stationary. The other chief type of cell in areolar tissue, the histiocyte, is not a mechanocyte but an amœbocyte. It is able to move and ingest foreign particles, and is then called a macrophage. Other types of cell are present in smaller numbers.

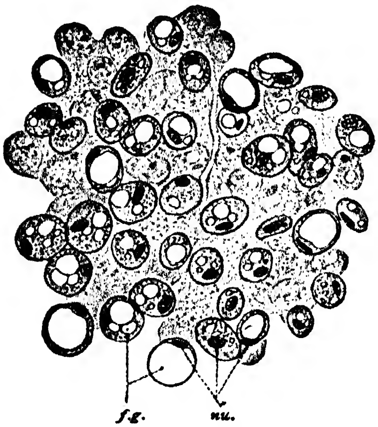


FIG. 26.11.—Part of one of the fat bodies of a frog, compressed and magnified, showing fat cells with fat globules in various stages.

f.g., Fat globules; *nu.*, nuclei.

The other types of connective tissue may all be looked on as derived from areolar tissue by modification of its cells, its fibres or its ground substance, or of more than one of these. In adipose

tissue large numbers of mechanocytes become so distended with fat that each appears as a large droplet of fat with thin cytoplasmic walls, and at one point a nucleus squeezed between the fat and the cell wall. The fat cells are probably specifically different from the fibroblasts, which are also present, and make white fibres which form a skeleton for the tissue. It is these fibres, together with the small amount of cytoplasm, which have to be removed when beef or mutton fat is clarified in the kitchen. Adipose tissue is chiefly found beneath the skin (where it makes the layer called panniculus adiposus), in the mesenteries, and round the kidneys. It is a food reserve, the fat being removed for oxidation or conversion into other substances when the food supply is low, but it also in places acts as a cushion, as in the eye-socket, and in naked mammals, such as man and the whale, the subcutaneous fat is an important heat insulator. The camel's hump is largely fat, which provides water when oxidised.

FIBROUS TISSUE

If there is in connective tissue little but collagenous fibres and the cells which form them we have white fibrous tissue. This is tough, strong, and non-elastic, and is found in parts of the body where these properties are important. The fibres may be arranged parallel to one another to form a cord, as in the tendons by which the pull of a muscle is transmitted to a bone or the ligaments which join two bones, or they may run criss-cross in one plane to form a sheet, as in the pericardium and the dura mater which covers the brain. The fibres of tendons are continuous with those which run in the general connective tissue of the muscle and bone, so that there is a very intimate connection between the two. Because of the high tensile strength of white fibres—of the order of 10,000 lbs. per square inch, which is similar to that of oak or cast iron—tendons seldom break, which is a good thing, as they regenerate only slowly. In elastic tissue little is present but yellow fibres, and it is accordingly found where elasticity is important. It may form cords, as in the ligamentum nuchæ by which the skull is attached to the cervical vertebræ, or sheets as in the walls of the trachea, lungs and arteries. Elastic fibres in the skin keep it taut and smooth and cause the edges of wounds to gape. Their deficiency in the aged allows the formation of wrinkles.

Where a connective tissue comes to a surface, as where it comes in contact with an epithelium, its constituents are usually condensed to form a sheet of material called a basement membrane.

CARTILAGE

More specialised mechanical tissues are the skeletal tissues, and of these there are two: cartilage and bone. Both are characterised by a large amount of tough ground substance, but this, as well as the type of cell, is different in the two tissues. The simplest type of cartilage, called hyaline on account of its clear or glassy appearance, is one of the easiest of all tissues to recognise. There are characteristic oval cells (Fig. 26.12), sometimes in groups of two or four where they have recently divided, and each cell or group is surrounded by a newly formed capsule of chondrin, which merges into the older chondrin farther away. Cartilage cells are derived from chondroblasts, which in their early stages are indistinguishable from fibroblasts. Some division of the cells goes on inside the tissue, but most of its growth takes place on the surface, where chondroblasts form a layer, the perichondrium. Hyaline cartilage, in spite of its appearance, does contain many collagenous fibrils, which, however, are not easily made visible. In adult mammals it is found only in a few places, such as the respiratory tract, where it makes the rings of the tubes, the ends of the ribs, and covering the articular surfaces of bones, but in the embryo, as well as in the adult frog and dogfish, there is much more of it.

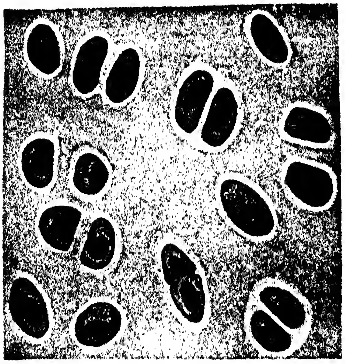


FIG. 26.12.—Cartilage stained and magnified, showing cells, some of which are in pairs formed by the division of a single cell, matrix, and the newly secreted part of the matrix, which forms capsules around the cells.

Fibrocartilage may be regarded either as cartilage in which there are many and conspicuous white fibres, or as fibrous tissue in which small patches of cartilage have developed. It is found between bones, as in the intervertebral discs, and sometimes in tendons. Elastic cartilage contains many yellow fibres; it is found in the epiglottis and Eustachian tubes, and especially

in the pinna or external ear trumpet. Cartilage is sometimes hardened by the deposition in it of calcium salts, when it is said to be calcified.

BONE

Bone contains cells called osteocytes, but its most striking feature is the fibrous and collagenous ground substance impregnated with complex calcium salts, largely phosphate. The

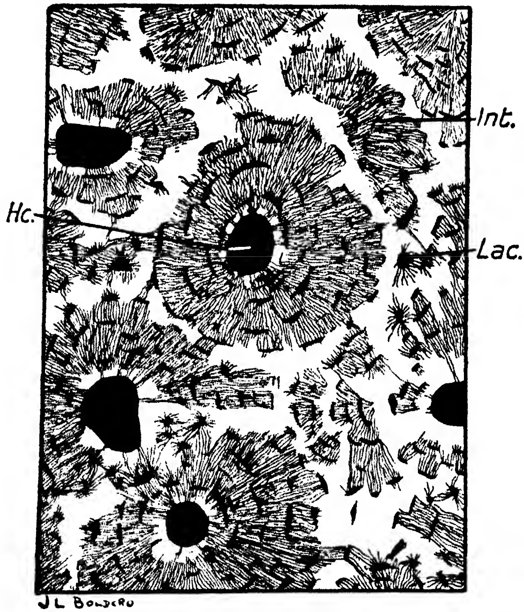


FIG. 26.13.—Section of adult bone (human femur).—From Le Gros Clark. *The Tissues of the Body*, 3rd edition, 1952. Clarendon Press, Oxford.

Hc., Haversian canal ; *Int.*, interstitial lamellæ ; *Lac.*, lacunæ. × *c.* 150.

fibres are arranged in lamellæ, and a transverse section of a hard bone shows that these form many-layered tubes called Haversian systems (Figs. 26.13 and 26.14). Between these and round the edge of the bone the lamellæ are irregular. The Haversian canal which runs down the centre of each system contains an artery, a vein, and a nerve, and some reticular tissue (p. 531). It branches and joins other canals, and some of these open into the space, if there is one, in the bone, which contains bone marrow (p. 531). The osteocytes are situated in spaces or lacunæ between the lamellæ ; these lacunæ communicate with each other, and with

the Haversian canal which they surround, by fine canaliculi. The centre of a bone often has the lamellæ irregularly arranged, with large spaces containing marrow; it is called cancellated, while that with the regular Haversian systems is said to be hard, or compact.

Bone is covered with a periosteum. The outer part of this is a connective tissue sheath, but below this is a highly vascular

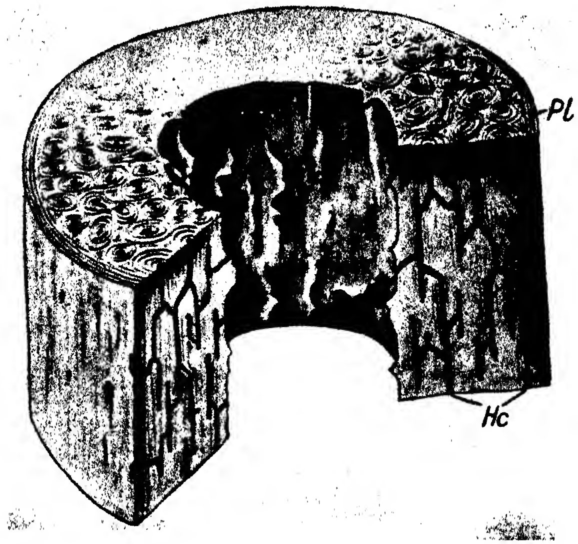


FIG. 26.14.—Diagram to show the lamellar structure of bone. The Haversian systems are represented greatly out of scale to show their arrangement in a long bone.—From Le Gros Clark, *The Tissues of the Body*, 3rd edition, 1952. Clarendon Press, Oxford.

Hc., Haversian canals; *Pl.*, peripheral lamellæ.

layer with many osteoblasts, cells which form bone partly by liberating a phosphatase enzyme which precipitates calcium phosphate from a calcium hexose phosphate circulating in the blood. As the periosteum is on the outside of the bone, the latter must grow chiefly on the surface. There is change of shape of a bone during life, and growth is assisted by the erosion of material already formed, and in this the chief agent is probably a special type of cell called an osteoclast. Some bones take the place, topographically and functionally, of embryonic cartilage, and are called cartilage bones, while others are formed in

unspecialised connective tissue and are called membrane bones. Histologically there is no difference between the two, and the cartilage of the former is dissolved before the bone is formed.

Although cartilage is the chief skeletal material of the most primitive existing fishes and precedes bone in ontogeny, bone is, so far as is known, at least as old a tissue, for it makes most of the skeleton of the earliest known vertebrates, the pteraspids and cephalaspids of the Silurian and Devonian periods. The bony exoskeleton of these is presumably represented by the membrane bones of the head and by the dentine of teeth and the placoid scales of the dogfish. Dentine has a structure somewhat similar to that in bone, though usually without blood vessels, and in fishes many transitional stages between the two are found. The cement of the teeth is also a modified bone.

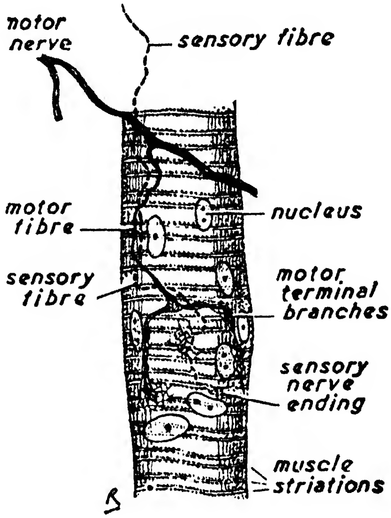


FIG. 26.15.—A piece of striped muscle fibre with nerve-endings upon it.—From Thomson.

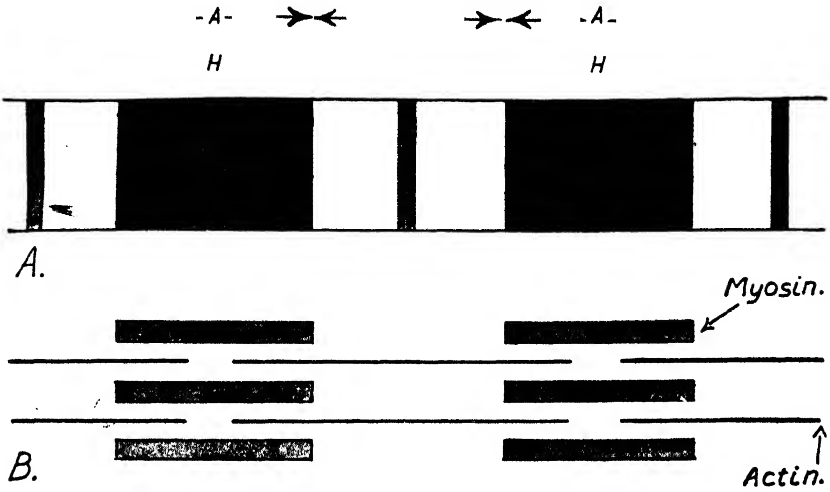
A motor nerve gives off motor nerve fibres which lead to branched motor-endings—terminal arborisation.

A sensory nerve-ending is shown from which impulses are carried by sensory fibres to a sensory nerve.

MUSCLE

The remaining mechanical tissue is muscle. There are three sorts of this in vertebrates, differing both structurally and physiologically. We will take first the muscle which is generally found attached to the bones. From this fact it is called skeletal, from its embryological origin it is called somatic, from its appearance striated or striped, and from its physiology, voluntary. Any of these terms may be used, but in zoology, as distinct from human anatomy, the last is best avoided, as we know little of the will-power of a frog or a fish or even of a mouse. The unit of striped muscle is the muscle fibre, which is not a cell but a syncytium (Fig. 26.15). The length of an average fibre is about 2·5 cm. and its diameter 0·05 mm., but there are many both larger and smaller. On the outside is a sheath, the sarcolemma, which encloses a liquid sarcoplasm

in which are a number of myofibrils and many nuclei. Each myofibril is made up of solid rods of two sorts. Thick rods of the protein myosin are arranged in such a way that each is surrounded by six other thick rods and six thin ones (Fig. 26.16, *C*). The latter



C.

FIG. 26.16.—Diagrams of the structure of voluntary muscle, based on A. F. Huxley.

A, longitudinal section, showing A and I bands, and H and Z lines; B, longitudinal section (electron microscope), showing actin and myosin filaments corresponding to the bands and lines in *A*; C, transverse section (electron microscope), showing the large filaments of myosin and small ones of actin.

are of another protein, actin, and are arranged so that each is surrounded by three other thin rods and three thick ones. The rods are not continuous through the fibre, but overlap in such a way as to give the banded appearance (Fig. 26.16, *A* and *B*). The dark or A bands are doubly-refracting, the light or I bands are not. In contraction the actin rods slide into the spaces between the

myosin rods, probably with formation of the compound acto-myosin, and after that there is probably folding of the molecules as shown in the model of Fig. 26.17. Red muscle fibres have more sarcoplasm and fewer fibrils, the nuclei are more scattered and the cross striations are less distinct, than in white muscle fibres. The two are generally found mixed in the muscle, and the red

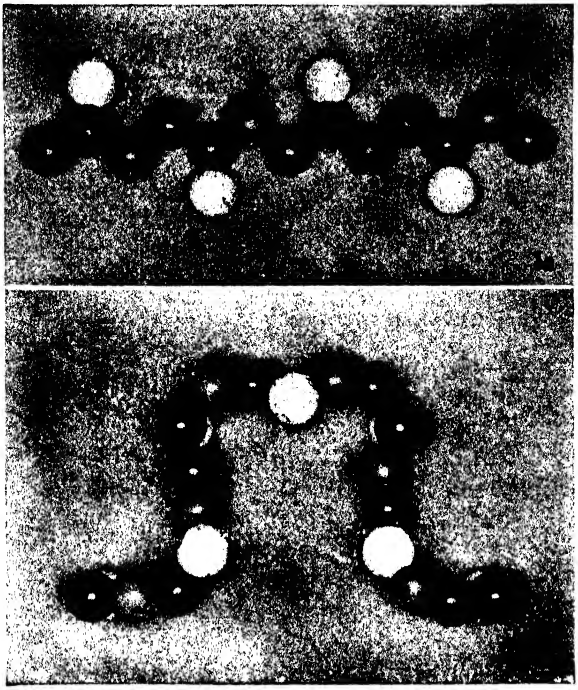


FIG. 26.17.—Skeleton models of peptide chains such as those of myosin.—From Astbury, in Le Gros Clark and Medawar, *Essays on Growth and Form*, 1945. Clarendon Press, Oxford.

1*a*., in straight form; 1*b*., in a folded form. White balls represent side chains.

fibres have a slower and more sustained contraction. Their colour is due to myohæmoglobin, which, like the related hæmoglobin of the blood, can hold oxygen and give it up when it is needed.

Muscles make up the flesh or meat of the body. They are well supplied with blood vessels, which do not penetrate the sarco-lemma. Motor nerve fibres do pierce this sheath, and end in branched motor end organs in the sarcoplasm, where they probably induce contraction by the liberation of a chemical

ubstance (Fig. 26.18). A smaller number of sensory nerve fibres end in modified muscle fibres, the muscle spindles, which respond to the stretching of the muscle. Muscle fibres are bound together by areolar tissue into small bundles or fasciculi, and these again into individual muscles. The toughness of meat depends largely on the amount of the connective tissue and especially on the

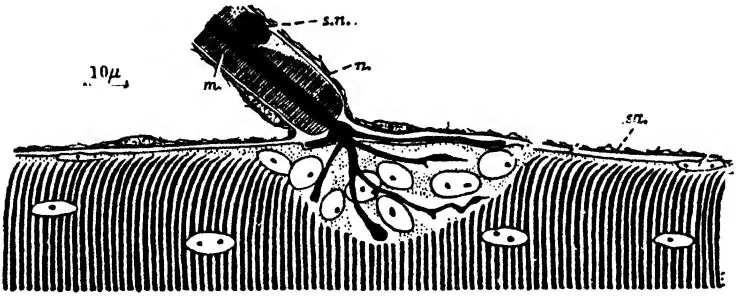


FIG. 26.18.—Diagrammatic representation of a motor end-plate in a muscle.—From Le Gros Clark, *The Tissues of the Body*, 3rd edition, 1952. Clarendon Press, Oxford. After Gutmann and Young.

m., Myelin sheath ; *n.*, neurilemma ; *s.n.*, nucleus of Schwann cell ; *s.a.*, sarcolemma.

proportion of white fibres which it contains. The connective tissue of a muscle is continuous with that of its tendon, and that in its turn, as we have seen, with that of bone, so that the contraction

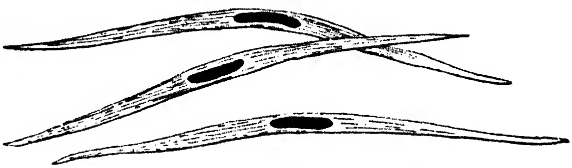


FIG. 26.19.—Isolated plain muscle fibres, showing nuclei.—From Le Gros Clark, *The Tissues of the Body*, 3rd edition, 1952. Clarendon Press, Oxford.

of the muscle is transmitted directly to the bone which it is to move.

The syncytial muscle fibre is produced by the division of the nucleus of a single connective tissue cell.

Visceral, smooth, plain or involuntary muscle is chiefly associated with the alimentary canal, the excretory system and other internal organs. Its unit, the smooth muscle fibre (Fig. 26.19) is a single spindle-shaped cell, without cross-striations. Fibrillæ

can be made out on treatment, but there is no true sarcolemma. Smooth fibres are smaller than striated fibres, not more than half a millimetre long. They are usually arranged in sheets or tubes rather than in bundles, and their period of contraction is longer than that of striped muscles. There is a double motor innervation from sympathetic and parasympathetic nerves, the former inhibiting and the latter promoting contraction. Nerve cell bodies, as well as fibres, are present in the muscles of the gut, so that there are networks or plexuses. As in skeletal muscle, the terminal fibres penetrate the cytoplasm. Smooth muscle shows great

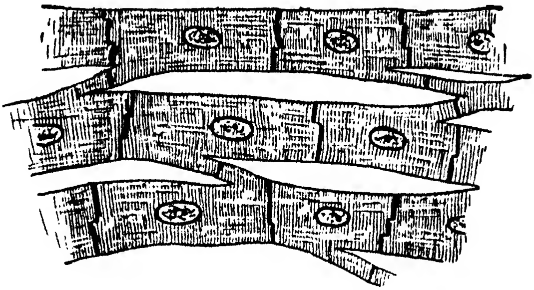


FIG. 26.20.—Diagram of cardiac muscle, showing nuclei, and side branches which give syncytial continuity.—From Le Gros Clark, *The Tissues of the Body*, 3rd edition, 1952. Clarendon Press, Oxford.

ability to contract without nervous stimulation, which is presumably why it needs two sets of nerves. The smooth muscle of molluscs has been shown to have, almost certainly, a sliding type of contraction similar to that of skeletal muscle, but the mechanism of vertebrate smooth muscle is still obscure.

The muscle of the heart, or cardiac muscle, is unique, and in many ways it is intermediate between smooth and striped muscle. The fibres branch and join, so that the whole mass of muscle forms a syncytium. Nuclei, cross-striations and fibrils can be seen, as well as cross walls which look like, but are probably not, cell walls, in spite of the fact that they separate the nuclei (Fig. 26.20). The heart in the embryo begins contracting before it has any nerve supply, but its control in the adult, like that of smooth muscle, is by double innervation. Since it is a syncytium, the whole heart must act at once, within the limits of the time of transmission of an impulse.

BLOOD

Thirdly and lastly we have the tissues which are based on the amœbocyte. They correspond fairly accurately to what are also called the fluids of the body because the ground substance is liquid, not solid. It is obvious that an amœbocyte can only show its properties fully in a liquid medium. First and most important

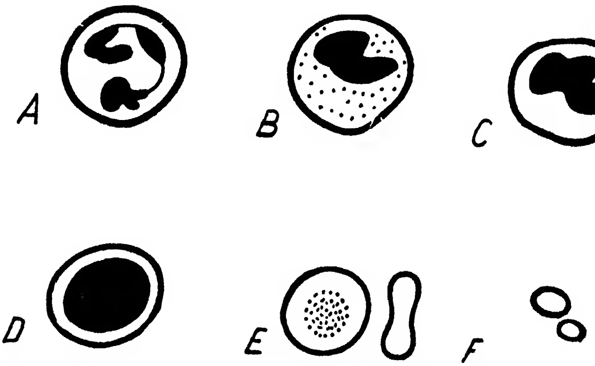


FIG. 26.21.—Blood cells.—Adapted from Whitby and Britton.

A and *B*, Polymorphonuclears; *C*, monocyte; *D*, small lymphocyte; *E*, erythrocyte, in face and edge view; the shading is conventional and represents the hollow in the surface; *F*, platelets. × 1,000.

is the blood. The liquid matrix is called plasma, and is an aqueous solution containing the ions of sodium, potassium, calcium, magnesium, chloride, phosphate, sulphate, and carbonate, together with glucose and other organic compounds, and a protein called fibrinogen, which together depress its freezing-point by 0·6° C. It is buffered, having in the arteries a pH of 7·3 to 7·45. When blood is shed, or the tissues are damaged, there is formed in it, by a complicated series of reactions that are imperfectly understood, a protein called thrombin. This changes fibrinogen to threads of insoluble fibrin, which form a network in which the cells become entangled, so that a clot is formed and bleeding stops. When drawn blood is clotted there is left a clear liquid which is plasma without its fibrinogen; it is called serum.

Blood is coloured red by the pigment hæmoglobin, which is entirely confined within small bodies called erythrocytes, red blood corpuscles, or simply red cells. Each, in man (Fig. 26.21), is a biconcave circular disc about 7.5 μ in diameter, so that it is shaped like an ordinary double concave lens. Its outer envelope

is semipermeable, as is shown by the ease with which it alters its shape in solutions of different strengths. It appears yellow, not red, under the microscope, why is not known, and piles of the cells tend to collect together to form rouleaux, which look like piles of pennies. There are about five million red cells per cubic millimetre in man, rather fewer in woman. In all other vertebrates the red cell is oval and contains a large nucleus, but in mammals this has been lost and the corpuscle seems to contain little or nothing but a colloidal solution of hæmoglobin. It is doubtful if it can justifiably be called living. The primitive oval shape of the red cells of lower vertebrates (but not the nucleated condition) is found in the Camelidæ alone amongst mammals.

A little of the carbon dioxide carried by the blood is in solution, most is combined as bicarbonate, and some is combined with hæmoglobin.

Hæmoglobin is one of a class of substances called respiratory pigments which convey oxygen from regions of high pressure, such as the surface of the body or lungs, to places where the pressure is low, such as the active glands and muscles. They do this by combining reversibly with oxygen in such a way that, in accordance with the Law of Mass Action, the compound is formed or dissociated as the concentration of oxygen changes through a range that runs, usually, from a maximum rather less than the partial pressure in the atmosphere (about 150 mm. mercury) to a minimum of about half this. The equation for hæmoglobin may be written formally as

$$Hb+4O_2 \rightleftharpoons HbO_8$$

but the four oxygen molecules are added successively, and some irregularities lead to the relationship between the proportion of the hæmoglobin present in the oxygenated form (oxyhæmoglobin) and the partial pressure of oxygen being a sigmoid curve. It is obvious that as the partial pressure falls from the 120 mm. or so in the alveoli of the lungs in man, oxyhæmoglobin will dissociate so that oxygen becomes available for chemical reactions.

Less numerous than the red corpuscles are the white cells or leucocytes, of which there are about 7,000 per cubic millimetre. They are nucleated and amœboid, and are classified by their nuclei and staining reactions into five or six different types. About seventy per cent. of them are polymorphonuclears (Fig. 26.21), 10 μ or a little more in diameter, and with a large lobulated

nucleus. They are highly phagocytic and are specially numerous in places where there is bacterial infection.

Blood platelets, or thrombocytes, are small particles of cytoplasm, 2 μ in diameter, of which there are about 200,000 per cubic millimetre. Their function is doubtful.

LYMPH

Plasma and white corpuscles are able to escape from the finest blood vessels into the surrounding connective tissue, a process known as diapedesis, and it is presumably from this source that the ' tissue fluid ' of the body is derived. In a healthy body, however, it is so difficult to detect in areolar tissue that many people have denied its existence. In pathological conditions, such as blisters and dropsy, it quickly accumulates, and on theoretical grounds is almost certainly always present. The passage of leucocytes through the walls of capillaries, where they have been filmed forcing their way between the cells, has been observed, and this supports the view that the histiocytes of connective tissue are simply white blood corpuscles. It is obvious that this leakage from the blood vascular tissue could not go on indefinitely unless there was at some point a return. This takes place through the lymphatic system. All over the body is a tree-like arrangement of small tubes ; their ends are closed, but the major trunks open into the veins at a number of points. In these vessels runs lymph, which is effectively blood minus red corpuscles and many of the white, and it presumably gets into them by the same means as that by which it escaped from the capillaries. Its return flow is directed by valves, but these are absent from the frog and other cold-blooded vertebrates, which possess instead contractile lymph hearts (p. 373). Most of the lymph passes into the left innominate or internal jugular vein, but there are subsidiary openings into the veins of the right side, and in many mammals there are others as well. The lymph vessels are hardly to be seen in dissection, as even in man the largest of them, the thoracic duct, is only two or three millimetres in diameter, and their walls are extremely thin.

Before opening into the main ducts all lymphatic vessels pass into structures generally called lymph glands, although lymph node is a better term since they are not known to have any glandular function. They are numerous in the inguinal and

axillary regions and in the neck, where their swelling in bacterial infection is known to most people. Each is a capsule containing large numbers of white corpuscles of a type called the lymphocyte, with strands of connective tissue running amongst them. Also present, and making a network, are cells similar to the histiocytes or macrophages of areolar tissue. The whole material of a lymph node, on account of its fine netted structure, is sometimes called reticular tissue and classified as a subdivision of connective tissue. As, however, most of its cells are amœbocytes, the alternative name of lymphoid tissue is preferable. Other parts of the body, with a structure somewhat similar to that of lymph nodes, are the spleen, thymus and bone marrow. The chief function of all these organs is the formation of blood corpuscles. The lymph nodes make lymphocytes, and pass them into the circulation ; the bone marrow, which occupies the centres of hollow long bones and the spaces of cancellous bone, makes red corpuscles. It is possible that lymphocytes are their raw material, and certainly the nuclei of the cells are lost before they are passed into the blood. The marrow also makes white corpuscles of many types, and other sources of them are the liver and spleen.

ORGANS

While the unity of a tissue is structural, so that wherever in the body it may occur it can be recognised by its appearance, that of an organ is topographical and usually physiological. It is a localised part of the body, and it carries out a single function, or rarely two or three functions. To do this it usually contains several tissues, and although one only of these may be concerned in the fundamental process which the organ carries out, without the other ancillary tissues the function could not be efficiently performed. For example, the essential tissue of a gland is the secretory epithelium, but the gland cannot function properly unless it has blood vessels which bring the raw materials of the secretion, and nerves which control its discharge. A gland must therefore contain many tissues besides epithelium.

SKIN

We have already, in describing the tissues, touched on the structure of various organs. A few of the more important will now

be considered more formally. First we may take the skin, which in mammals at least is well enough developed to be looked on as an organ. It separates the body from the outside world, so that impermeability must be one of its properties, but this impermeability is controlled and modified by the existence of pores and by modifications of the cells. The structure of skin as seen in section is shown in Fig. 26.5. The outer part or epidermis has already been described as an example of a stratified epithelium. We need only add here that it is pierced by hairs and by the ducts of sweat glands, and that its basal layers contain, in addition to the ordinary polyhedral cells, many which are branched. These are called melanocytes or dendritic cells, and it is they alone which in pigmented skin form melanin. In white skin the cells are present, but they are unable to make pigment. Below the epidermis is the dermis or corium, which is connective tissue of mesodermal origin, mainly white fibres but with some elastic fibres in its outer parts. In it run blood vessels, lymphatics and nerves. Below it is a layer of subcutaneous adipose tissue, and below this again more connective tissue making the superficial fascia. In places the dermis shades imperceptibly into this. In places, as for example, the penis, scrotum and nipple, and especially in mammals such as rodents, the dermis contains smooth muscle, and in the skin of the cat and in that of the face of man there is voluntary muscle. Hairs appear to take their origin from the dermis, but are in fact epidermal structures. A downgrowth from the surface forms a follicle, and from the base of this the hair grows up, so that it projects above the surface. Into the base have grown blood vessels and other tissues of the dermis to form a papilla. A hair is made of many cells, typically arranged to form a cylinder round a softer core. It consists largely of keratin, and has a variable amount of pigment. In old age the core may break down and become filled with air bubbles, which give a white appearance. Opening into the hair follicles are sebaceous glands, which are derived from the stratum of Malpighi and break down to form a mixture of lipoid material and cell débris called sebum. This makes a waterproof and antiseptic film which is squeezed over the skin when the smooth muscles attached to the hairs contract. Its lipoid part, which consists mostly of esters, not of glycerol but of higher alcohols such as cholesterol, is well known in the form of wool-wax or lanoline, which is the chief constituent of face-creams and brush-

less shaving cream ; a similar material is found in the oil glands of birds. On exposure to sunlight some of these esters are converted to vitamin D, and in some animals licking of the fur may be an important source of this.

Sweat glands are long tubes, of which the deeper and secretory parts are coiled in the lower part of the dermis, or, on the palms and soles, below this in the superficial fascia. Their secretion is more than ninety-nine per cent. water, with a little sodium chloride and negligible amounts of urea and other organic substances, so that they are of no importance in excretion. The function of the sweat glands is to control the temperature of the body by providing water which can evaporate, and it is only when the skin temperature has been raised above normal by exercise or heat, or in emotional excitement, that visible sweating begins.

The structure of the skin of the frog, which is without hairs and sweat glands, but possesses other glands of its own, is shown in Fig. 22.3. The scales of reptiles are thickenings of the epidermis, and feathers are comparable in their origin to hairs. Claws, nails, hooves and horns are also epidermal structures. The epidermis of teleosts is unusual in that it apparently contains no keratin.

ALIMENTARY CANAL

The alimentary canal has already been mentioned as including columnar epithelium and smooth muscle. In most parts at least four layers, with subdivisions, may be distinguished in the wall (Fig. 26.22). On the inside is the epithelium, often with glandular developments. Surrounding this is a layer of areolar tissue called the submucous coat, in which run blood vessels and lymphatics, and the autonomic nerve net called Meissner's plexus ; between the submucous coat and the epithelium there is, in the small intestine, a layer of smooth muscle which produces contractions of the villi, or projections into the lumen. Outside the submucous coat is the muscular layer which makes up most of the thickness of the wall. Typically there are on the inside smooth muscle fibres running circularly, outside these longitudinal fibres, and between the two a nerve net called Auerbach's plexus. In the small intestine each set of muscle fibres runs strictly in the form of a left-handed screw, one set being of high and the other of low pitch. The two sets are complementary and together lead to the

waves of contraction in the intestine called peristalsis. Increases in the circular muscle at various points form sphincters, by contraction of which passage of material from one part of the

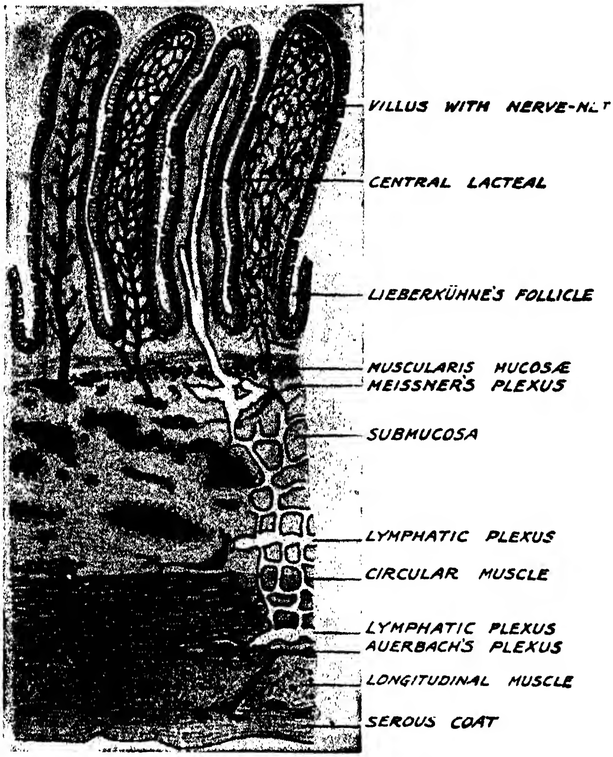


FIG. 26.22.—Diagrammatic section through the wall of a mammalian small intestine to show vascular and lymphatic arrangements.—From Yapp, *An Introduction to Animal Physiology*, 1939. Clarendon Press, Oxford. After Schaffer.

canal to the next may be checked. Outside the muscular layers is the serous coat, which is continuous with the mesenteries. It consists of connective tissue, with, on its outer surface, a single layer of flat, closely-fitting cells very similar in appearance to pavement epithelium ; this is usually regarded as a condensation of connective tissue, and called a mesothelium.

LIVER

The structure of the liver is very difficult to make out. It consists of sheets of tissue, which in mammals are one cell thick,

branching and anastomosing and surrounding spaces. In these lumina are blood vessels, with scarcely visible walls, which are the capillaries of the hepatic portal system. Fine canaliculi of the bile duct surround the cells, and at places, branches of the hepatic artery and vein join the capillaries.

The liver is usually interpreted as a gland that arises as a diverticulum of the gut, but this is probably incorrect. Its cells are derived directly from endoderm (in Amphibia from those containing much yolk) and in most species from mesoderm as well. Only in a few, such as the chick, does the bile-duct arise

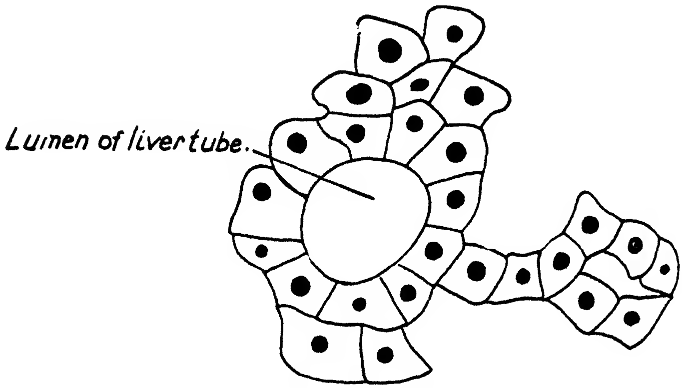


FIG. 26.23.—A small portion of the liver of a pig in section × c. 300.

as an outgrowth of the gut; in most it develops from the liver tissue and joins the gut secondarily. The bile is secreted into fine passages which form a reticulum between the cells and so goes by the bile-duct to the intestine.

The main function of the liver is to take raw materials from the blood stream, change them chemically, and return both useful products and waste material to the blood; it deals with excess amino acids by the linked processes of transamination and deamination. In the first there is a reaction with α-ketoglutaric acid in which the amino group is transferred to this to form glutamic acid, while the residue of the amino acid is left as an α-ketoacid such as pyruvic. In the second, glutamic acid is oxidised to α-ketoglutaric acid, which is thus restored, and ammonia, which is mostly converted to urea by a cyclic process called the ornithine cycle.

The hexoses produced by digestion are built up, by a relatively

simple reaction, into glycogen, which is stored in the liver cells. They can also be broken down, by a series of reactions known as glycolysis, to pyruvic acid, which has three carbon atoms, and this is converted to acetylcoenzyme A (effectively acetic acid, a 2-carbon compound, united to pantothenic acid, one of the B-vitamins). A complicated series of reactions, called the tricarboxylic or citric acid cycle progressively oxidises this. As pyruvic acid, acetylcoenzyme A, and other constituents of the cycle are produced from fats or proteins, all the chief classes of foodstuff are caught up in this cycle for the provision of energy. No free oxygen is used, but oxidation takes place by the successive addition of water and removal of hydrogen, with production of some carbon dioxide. For the removal of hydrogen, substances known as hydrogen acceptors, with which it can combine, are necessary. The most important of these is coenzyme I (diphosphopyridine nucleotide, DPN), which is a derivative of nicotinamide, one of the B-vitamins. Others are flavinmononucleotide (FMN) and riboflavin-adenine-dinucleotide (FAD), both derived from riboflavin, another B-vitamin.

Most of these reactions are reversible, and their direction follows the needs of the animal, glycogen and fat being built up when food is in excess and oxidation taking place when energy is required. The control is affected in part by a complicated series of hormones. Insulin from the pancreas, which is liberated into the blood whenever the concentration of glucose in it rises, accelerates all the reactions that tend to remove glucose—its synthesis to glycogen and fats and its oxidation. Glucagon, also from the islet tissue of the pancreas, and adrenaline, from the adrenal medulla, stimulate the breakdown of glycogen to glucose, and there are other effects of these and other hormones.

The same or similar reactions go on in other tissues. The high chemical activity of the liver is connected with the large numbers of mitochondria that its cells contain.

The formation of bile, which contains breakdown products of hæmoglobin and is marginally useful in the digestion of fat, is perhaps secondary.

PANCREAS

The pancreas (Fig. 26.24) has a more obviously diverticular nature. It is a compound tubuloalveolar gland, that is, it branches many times and both the finer tubules and their terminal

swellings or alveoli are secretory. The cells are somewhat polyhedral. The islets of Langerhans, or islet tissue of the pancreas, are masses of cells which have become separated from the ducts and are endocrine in function, producing the insulin and glucagon just described.

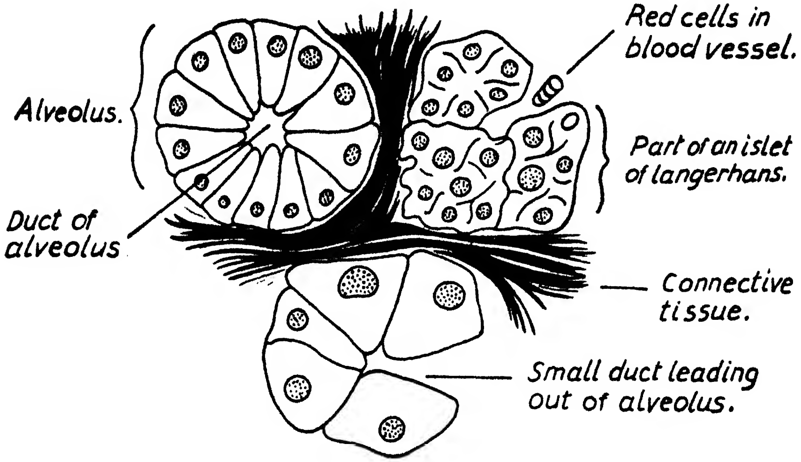


FIG. 26.24.—A small portion of the pancreas of a guinea-pig in section. × *c.* 400.

LUNGS

The lungs also are outgrowths of the alimentary canal. In the frog each is a simple sac, but in the mammal the original diverticulum has become very finely divided. Each terminal bronchiole expands into a group of air sacs or infundibula, and each of these has its wall pushed out into several pimples, called air cells or alveoli, so that the final appearance is not unlike that of a bunch of raisins. The alveoli are lined by a thin pavement epithelium, and outside this are the blood vessels and some connective tissue with yellow fibres. Covering the whole lung is a serous coat similar to that of the gut. The bronchi have a ciliated epithelium, and outside that there is elastic tissue, plain muscle, and fibrous tissue, in that order. In the larger tubes the fibrous tissue contains cartilage. It is the contraction of the muscle, which forms an irregular network, and of the elastic fibres, which forces air out of the lung in the so-called passive expiration of mammals.

SPINAL CORD AND NERVES

A section of the spinal cord (Fig. 26.26) shows that the nervous tissue is surrounded by membranes or meninges. On the outside

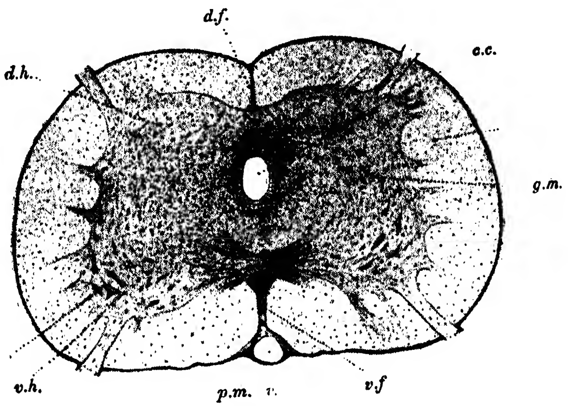


FIG. 26.25.—A transverse section of the spinal cord of a frog.

c.c., Central canal; *d.f.*, dorsal fissure; *d.h.*, dorsal horn; *g.m.*, grey matter; *n.c.*, large nerve cell; *p.m.*, pia mater; *v.*, vein; *v.f.*, ventral fissure; *v.h.*, ventral horn; *w.m.*, white matter.

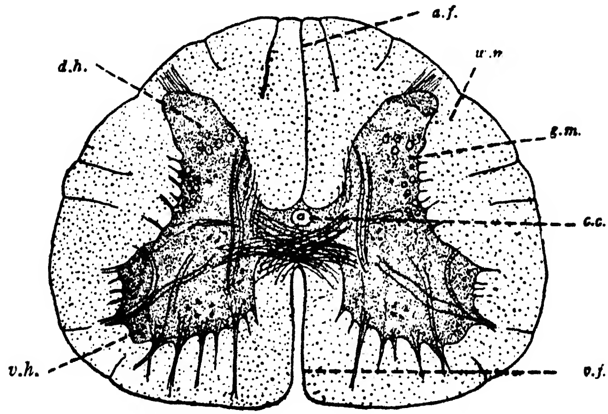


FIG. 26.26.—A transverse section of the spinal cord of man, taken through the lumbar region, between nerves, with the pia mater removed.

Lettering as in Fig. 26.25.

is the dura mater, which is fibrous and vascular; inside this are the arachnoid, and then the pia mater, consisting of flattened cells. Between these two, and in places between the arachnoid

and dura mater, are spaces containing cerebrospinal fluid, which is secreted in the ventricles of the brain and returns to the venous system. The nervous tissue is divided into an outer

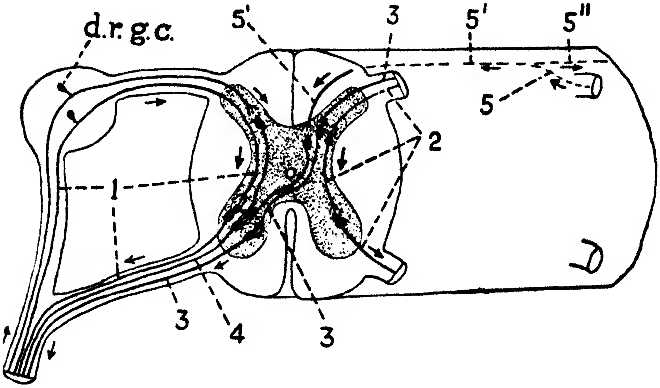


FIG. 26.27.—A diagram of fibres entering and leaving the spinal cord, showing various tracks along which impulses may be conducted in the 'exchange' system which it constitutes. The arrows show the direction of impulses.

Note that where the terminal branches of the axon of one neuron meet the dendrites of another the two are not continuous but interlace, so that the nervous impulse must pass an interruption in its track. This arrangement is called a *synapse*.

1. The simplest track, one afferent and one efferent neuron; 2. an intermediate neuron is concerned; 3. the track crosses the cord, so that an impulse is discharged along a nerve on the opposite side; 4. a neuron receives impulses from two others; 5, 5', 5", a fibre branches to affect neurons in different parts of the cord; *d.r.g.c.*, cells of dorsal root ganglion.

white matter, consisting mainly of nerve fibres, and an inner, somewhat X-shaped grey matter, consisting mainly of cell bodies. In the very centre is a small central canal. The brain is generally similar, with, in the hemispheres, a great development of the grey matter. Nerves (Fig. 26.28) are bundles of nerve fibres bound together by connective tissue, first into funiculi and then into larger groups, the whole nerve being covered by an epineurium comparable to the dura mater. In the connective tissue of a nerve run blood

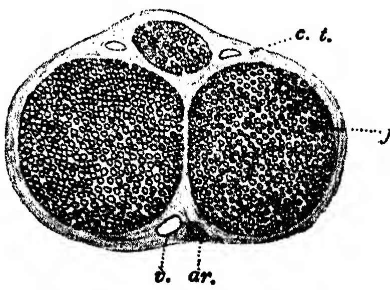


FIG. 26.28.—A transverse section of a medullated nerve of the frog, stained with osmic acid and magnified.

ar., Artery; *c.t.*, connective-tissue sheath or perineurium; *f.*, funiculus or bundle of nerve fibres; *v.* vein.

vessels, lymphatics and nerves—for even nerves have nerves—and there is often much fat.

SENSE ORGANS

In some parts of the body, such as the muscles and skin, sensory nerve fibres end in contact with cells of other tissues (muscle fibres, epithelia) which are in some ways sense cells, but it is perhaps safest to use this term only for a nerve cell which is specially modified to form part of a sense organ. In the olfactory membrane (Fig. 26.29) a number of nerve cell bodies are scattered amongst the epithelial cells, and their axons run inwards as the fibres of the olfactory nerve. In the retina (Figs. 26.30 and 26.31) things are more complicated. On the outside a pigmented epithelium prevents light from reaching the sensitive elements, or rods and cones, except from the proper direction. Each rod or cone is a process of a nerve cell, the bodies of which make the outer nuclear layer. From these run rod and cone fibres, which meet the dendrons of bipolar cells in the outer molecular or outer synapse layer. A bipolar is a cell with two processes. The bodies of the bipolars, which come next, make the inner nuclear layer, and next there comes the inner molecular or inner synapse layer, where processes of the bipolars meet dendrons of another set of cells, the bodies of which make the seventh or ganglionic layer. From this the axons run tangentially as nerve fibres which leave the eyeball as the optic nerve. As a result of the way in which the eye develops (Fig. 27.50) the layers are said to be inverted ; the sensitive elements are on the outside, light has to travel through two other layers of neurons to reach them, and the optic nerve has to leave by what is, in effect, a hole in the retina, so that it makes a blind spot which is insensitive to light. Between the rods and cones and their bodies is connective tissue, the outer limiting membrane, and inside the nerve fibres more connective tissue making the inner limiting membrane. The two sets are connected by fibres of Müller. In the inner synapse layer and amongst the nerve fibres are capillaries.

In the fovea, where rays from an object at which we are looking are normally focused, there are no rods, while the greater the distance from this the more of them there are, until at the periphery there are hardly any cones. Now the periphery is nearly colour-blind, but more sensitive to weak light than is the fovea

(it is sometimes possible to see a faint star only by looking to one side of it), so that it seems that while the rods are concerned with appreciation of low light intensities (twilight vision), the cones alone can detect colour. How they do this is still a matter of

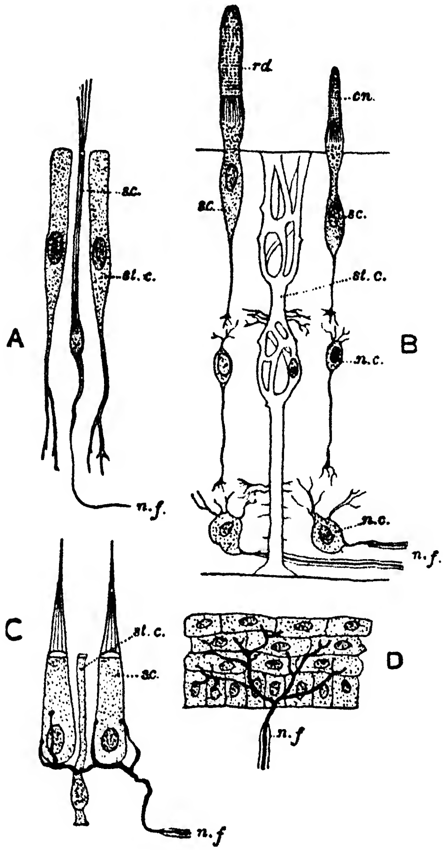


FIG. 26.29.—Examples of different modes of ending of sensory nerve fibres of the frog.

A, Cells from the olfactory epithelium. *B*, cells from the retina, much simplified. *C*, cells from one of the patches of sensory epithelium in the labyrinth, with which the fibres of the auditory nerve are connected. *D*, a portion of the epidermis, showing the ending of a nerve fibre.

D is ordinary stratified epithelium. *A*, *B*, and *C* are true sensory epithelia—forms of columnar epithelium adapted to the purposes of special senses. In these latter there can be distinguished *sense cells* and *supporting cells*. The sense cells bear processes of various kinds on the surface of the epithelium, and at their other ends come into relation with nerve fibres. In *A* the sense cell is prolonged into a fibre which runs in one of the olfactory nerves as a non-medullated nerve fibre (p. 515). In *B* also the sense cells are prolonged into fibres though these are connected with the nerve by the intermediation of other cells with whose processes their fibres interlock. In *C*, on the other hand, the sense cells are not continued into fibres, but are embraced by branches of nerve fibres belonging to cells in the ganglion of the auditory nerve. Thus they resemble *D*, where the nerve fibres have a similar relation to the cells of the epithelium. In the lower animals, such as the earthworm, the sensory nerve endings n the skin are usually of the type of *A* and *B*, rather than that of *C* and *D*.

c.n., Cone ; *n.c.*, nerve cells ; *n.f.*, nerve fibres : *rd.*, rod; *s.c.*, sense cells; *st.c.* supporting cells.

dispute. The action of the rods is connected with the breakdown of a pigment called visual purple, which is closely related to vitamin A ; deficiency of this vitamin is well known to cause

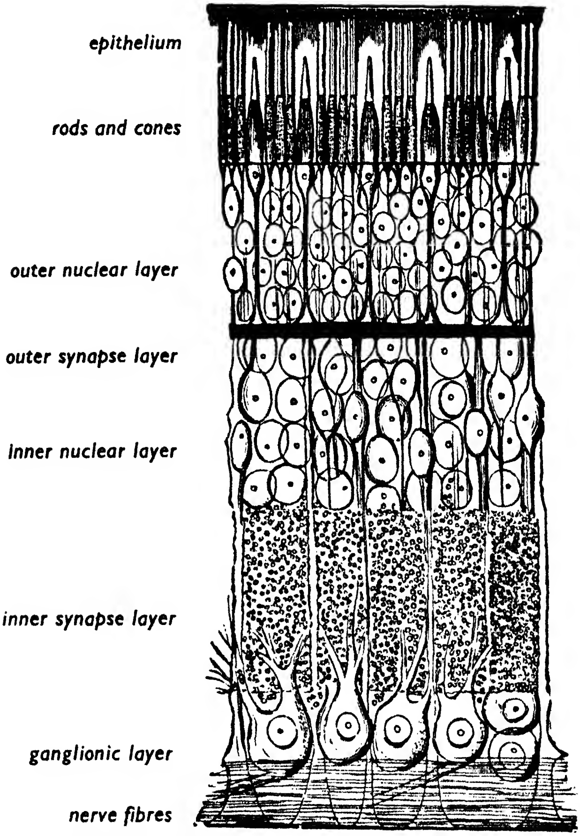


FIG. 26.30.—A transverse section of the human retina.—From Quain. *Elements of Anatomy.*

difficulty in seeing in dim light (' night blindness '). The sensitivity of the fovea is very nearly at the theoretical limit both in the intensities which will cause a response and in the size of particles which can be discriminated.

The sclerotic consists mainly of fibrous tissue, with pigmented connective tissue inside it. The cornea has fibrous tissue continuous with that of the sclerotic, and it is covered externally by a stratified epithelium and internally by pavement epithelium. It has nerves, but no blood vessels or lymphatics. The choroid,

which is richly pigmented, has three layers corresponding to the dura mater, arachnoid and pia mater. From it are formed the intrinsic muscles of the eye. The lens has an elastic capsule, and lens fibres formed from epithelium.

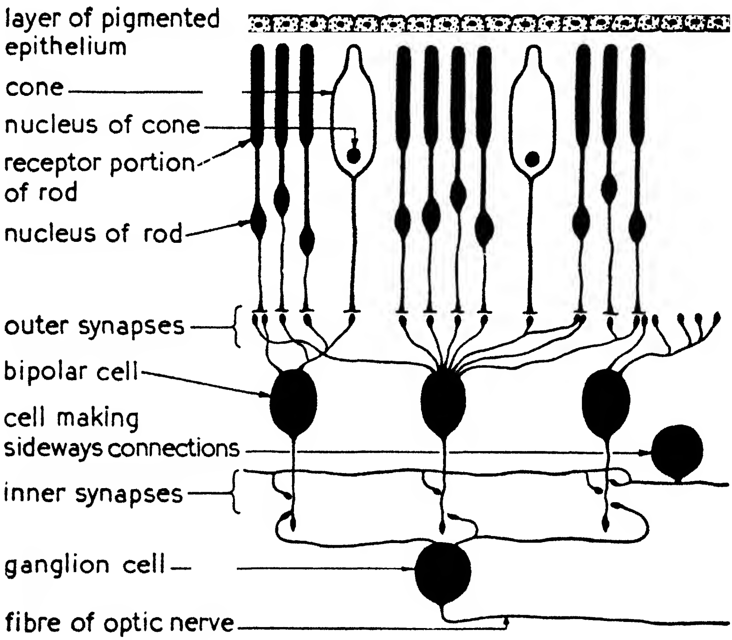


FIG. 26.31.—A simplified diagram of the nervous connections in the mammalian retina.—From Yapp, *An Introduction to Animal Physiology*, 2nd edition, 1960. Clarendon Press, Oxford.

BLOOD VESSELS

Arteries (Fig. 26.32) are lined by endothelium, consisting of flattened scale-like cells ; it is surrounded by a little elastic tissue, and outside this again is a thick coat of elastic tissue and plain muscle, and outside this again is collagenous tissue. The proportion of muscle to elastic tissue varies, and in general the larger the vessel the higher the proportion of elastic fibre. The great vessels near the heart are therefore able to take up the increased pressure caused by systole by an expansion followed by an elastic recoil-contraction. These appear as the pulse. In the finest arteries, the arterioles, there is nothing but muscle in the middle coat, and in the capillaries all the parts of the wall have gone except the endothelium ; the transition from the great

vessels through to the capillaries is of course gradual. The walls of veins are built on the same plan as those of the arteries, but there is much variation. It is obvious in dissection that of a pair of vessels running together to and from an organ the vein has a larger lumen and a thinner wall than the artery, although the outside diameters of the two are about the same. (The colour of the blood can more readily be seen in a vein, while an artery of any size is white or bluish, and an artery may usually be safely held with forceps, whereas the veins are too easily torn.) It is obvious that the larger lumen is made necessary by the fact that the velocity of the current in a vein is less than that in the

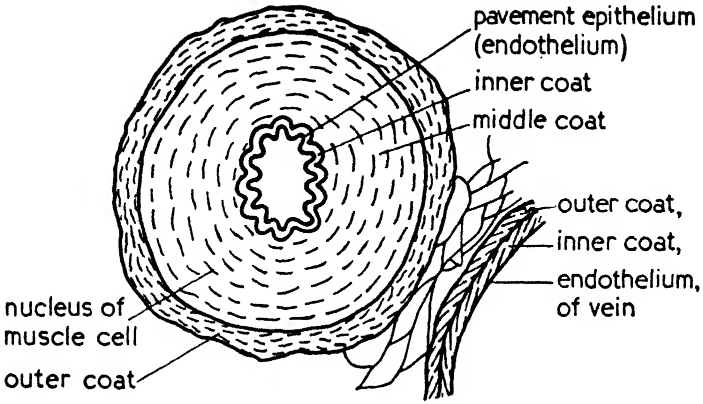


FIG. 26.32.—Diagrammatic transverse section of an artery and part of a vein of a rabbit. × *c.* 15. The endothelium and inner coat are thrown into folds through contraction of the muscular layer.

corresponding artery although the rate of flow (in volumes per second) is about the same; still waters run deep. In a typical vein there is relatively less muscle and elastic tissue and more collagenous tissue than in an artery, and the distinction between the two connective tissue coats is poor or absent. In other veins the amount of muscle ranges from much to nearly none, the differences being presumably and sometimes demonstrably of functional value. Where there is much muscle, as in the hepatic veins and those of the penis, the vein can contract so that its lumen is reduced and return flow of blood prevented. The valves which are present in many veins are made of folds of the endothelium with a little connective tissue between the layers. The finest veins, or venules, consist, like arterioles, of endothelium with a thin layer of supporting tissue on the outside.

THE KIDNEY

The vertebrate kidney consists of a large number of cœlomoducts which join together and have a common opening to the exterior. In mammals each cœlomoduct or tubule (p. 626) opens internally, not into the general cœlom but into a separate minute part of it, called a Bowman's capsule, into which is pushed a knot of blood vessels called a glomerulus. The capsules are lined by pavement epithelium, the tubules by cubical, and lower down, by columnar. The larger vessels, as we have seen, have transitional epithelium. A low power section of a kidney shows an outer cortex consisting mostly of the capsules and convoluted tubules, and an inner medulla, consisting of the collecting tubules leading to the pelvis of the kidney, where the ureter leaves. All the tubules are held together by areolar tissue.

MUSCLES AND BONES

The ways in which striped muscle fibres are joined together to form a muscle, and muscles joined to bones by tendons, have already been described. The contraction of a voluntary muscle generally moves one part of the skeleton on another ; the point where a muscle is attached to a relatively fixed part of the skeleton is called its origin, that where it joins a freely movable part its insertion, but these are somewhat loose and arbitrary terms, as according to the circumstances it may be one or the other bone which moves. To enable movement to take place there must be a joint, or in anatomical language, a diarthrosis. The bony surfaces of the articulation are separated from each other by hyaline cartilages, and these are in contact except for a thin lubricating layer of synovial fluid (Fig. 24.4). Enclosing the articular cartilages and the fluid is the synovial membrane, a mesothelium of connective tissue cells, so that the bones are separated by a bag-like space, the synovial cavity. Synovial fluid is very similar to blood plasma without colloids, but it also contains mucin, the lubricating protein. Besides its function in reducing friction synovial fluid probably also supplies food to the cartilage. In a symphysis, where there is slight movement, the bones are covered by plates of hyaline cartilage, and these are joined by fibrous tissue or fibrocartilage. In sutures the bones are interlocked by their wavy edges, as well as being joined by fibrous tissue, so

that movement is impossible. Sutures are usually completely obliterated in older animals by complete fusion of the bones.

GONADS

The ovary (Fig. 26.33) consists of a mass of fibrous tissue with some smooth muscle covered by the germinal 'epithelium'

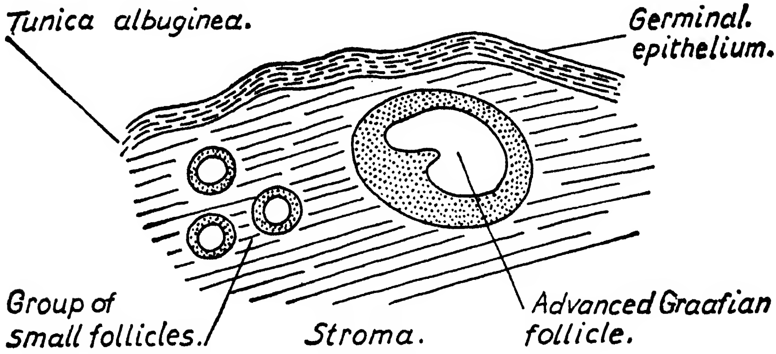


FIG. 26.33.—Part of a section of an ovary of a rabbit. × c. 30.

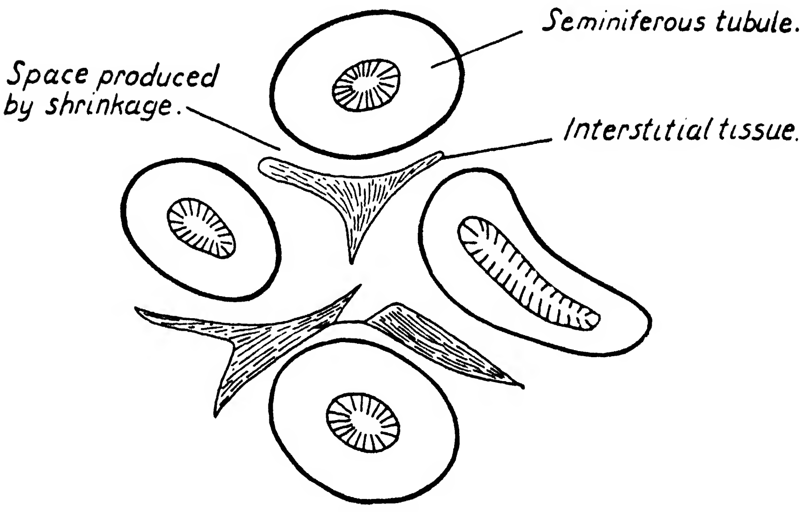


FIG. 26.34.—Diagrammatic transverse section of a part of a testis of a rat. × c. 25.

derived from undifferentiated endoderm. This sinks in at places and at each it becomes pinched off to form a mass of cells, one of which becomes an ovum. The others form a hollow Graafian follicle, consisting of a wall, the membrana granulosa, with at one place an inner swelling, the discus proligerus, which surrounds

the ovum. Round each follicle the connective tissue condenses as an outer wall, the theca. In most mammals all the follicles have been formed soon after birth.

The testis also consists largely of connective tissue, with a strong fibrous coat. The essential part of it consists of many

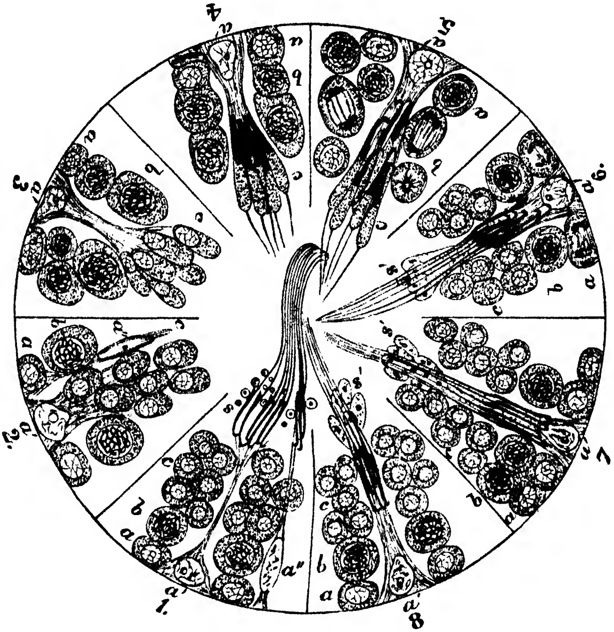


FIG. 26.35.—A diagrammatic representation of the spermatogenesis of the rat.—After Schafer.

Each of the numbered sections of the diagram represents a portion of the circumference of a seminiferous tubule at a certain stage of the process. In (1) the cells (spermatids) which result from the two successive maturation divisions of the spermatocytes, and eventually become spermatozoa, are seen in their earliest condition. In (2) they have become attached in groups to supporting cells (cells of Sertoli). In (3) to (8) they are becoming spermatozoa, of which their nuclei constitute the heads. In (1) again, they are ready to be set free.

a, and *a′ a″*, Lining epithelium cells of the tubules; *a* are 'spermatogonia,' which by division (seen in 6) throw off spermatocytes; *a′* and *a″* are cells of Sertoli, which support the spermatids; *b*, spermatocytes. These undergo the two maturation divisions (indicated in 5) whose ultimate products are *c*, the spermatids. The latter, in the process of development into spermatozoa, which they undergo after attachment to cells of Sertoli, throw off *s′*, portions of their cytoplasm which disintegrate (*s*).

convoluted seminiferous tubules, the cells in the walls of which form the spermatozoa (Fig. 26.35). The tubules join and pass into vasa efferentia, which are lined with columnar ciliated epithelium, and these in turn lead into the coiled epididymis, which is continuous with the muscular vas deferens. Also in the connective tissue are the interstitial cells, derived from the nephrotome, which produce the sex hormones.

27

THE CLASSIFICATION AND STRUCTURE OF VERTEBRATES

In earlier chapters we have described the dogfish, frog, pigeon, and rabbit, which are the types of vertebrate most often studied in elementary courses of zoology, but for a proper understanding of the way in which the vertebrate body is built we need to know something about other animals; in particular there is a big gap between the dogfish and rabbit which is only partially filled by the frog, an aberrant and unimportant creature which is dissected chiefly because it is (or was) cheap and plentiful. In this chapter we shall consider the chief organ systems in turn, showing their range in complexity and presumed course of evolution, but first we must have a classificatory framework to which to refer.

The Vertebrata or Craniata, the fourth subphylum of the Chordata (p. 308), are distinguished from the others by the possession of a bony or cartilaginous skeleton, part of which is arranged as a jointed dorsal longitudinal axis, the vertebral column or backbone, consisting of separate pieces called vertebræ; at the front end of this is a skull which partially or entirely encloses the brain. Characteristic features of the soft parts are the great development of the brain, and with it of the organs of sight, smell and hearing; a heart with at least one receiving and one pumping chamber; the respiratory pigment hæmoglobin in corpuscles; a small number of gill slits (seldom more than ten pairs); and an excretory system based on the cœlomoduct (p. 188). The notochord is usually lost in the adult and never extends to the anterior tip of the body. Most vertebrates have paired limbs, and possibly all the earlier forms had them, but as there are now several groups which are limbless this is not a very practical distinction.

Superclass I—Agnatha

The earliest known fossil vertebrates, from the Silurian and Devonian periods, have no jaws, and are placed in a separate super-class. The only similar living animals are a few semi-parasitic genera called lampreys and hagfishes, which are without

any trace of paired limbs. For convenience lampreys and hagfishes may be put together in the class Cyclostomata, but it is at least possible that they are descended from different fossil classes.

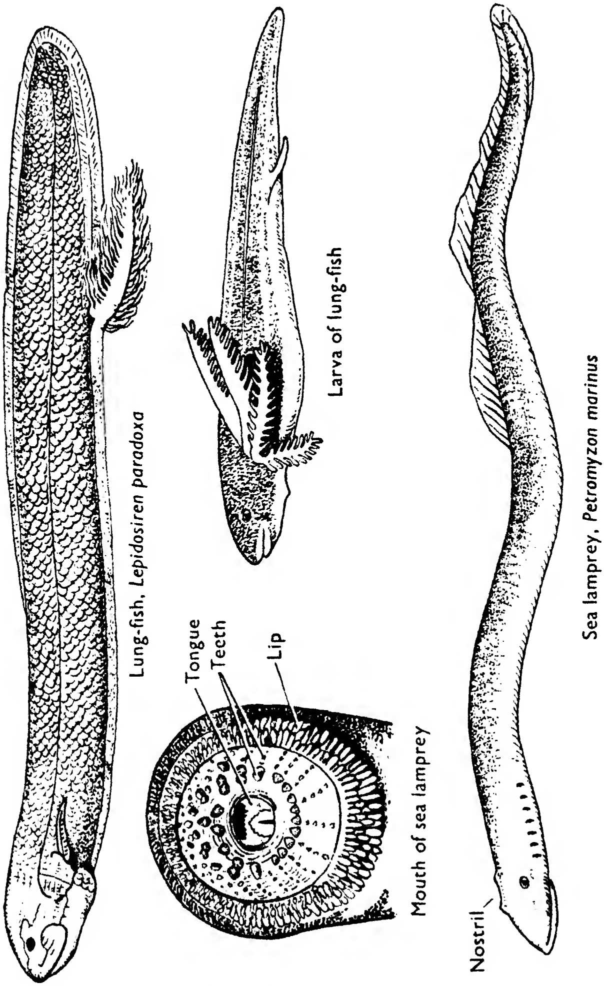


FIG. 27.1.—Lamprey and lung-fish.

Lampetra fluviatilis, the river lamprey, is tolerably common in some rivers, such as the Severn, and *Myxine glutinosa*, the hagfish, is found in British seas. The larva of lampreys, the 'ammocœte', has a ciliary method of feeding comparable to that of *Branchiostoma*.

SUPERCLASS II—GNATHOSTOMATA

The remaining vertebrates agree in possessing jaws, and are further distinguished from the Cyclostomata in having a double instead of a single nasal opening, and in possessing three, instead of two, semicircular canals. They are now generally placed in seven or eight classes, the former class Pisces, the fish, being divided into three or four groups which represent early divergences of the gnathostome stock.

CLASS I—CHONDRICHTHYES OR ELASMOBRANCHII

These are the cartilaginous fishes, and include the modern sharks, of which the dogfish is a good example, and rays and skates, in which the body is flattened and the tail reduced. They are difficult to define, but some of the chief characters of the modern forms are the absence of bone from the endoskeleton ; a valvular contractile conus arteriosus ; the presence of a large amount of urea in the blood ; plate-like gills ; absence of an operculum ; a spiracle ; absence of an air-bladder ; a heterocercal tail (p. 558) ; a spiral valve in the intestine ; claspers in the male ; and large yolky eggs laid in heavy cases. The extinct forms did not possess all these features. The only near-diagnostic character is the placoid scale, which has essentially the same structure as a tooth and contains dentine. If this material is regarded as a type of bone (p. 523) it is untrue to say that the elasmobranchs contain no bone. A number of Silurian and Devonian fossils have a bony exoskeleton, underneath which have been traced blood vessels and nerves of an elasmobranch pattern ; whether these fishes are regarded, as at first they were, as primitive Chondrichthyes, or whether they are placed in a separate class, the Placodermi or Aphetohyoidea, does not much matter, but it is clear that the earliest known gnathostomes had much bone and that the condition of the present-day cartilaginous fishes is probably secondary. Their loss of armour may be connected with the development of actively predaceous habits. In spite of their specialisation in this direction the modern sharks represent, in most of their soft parts, the best that we can find as an example of a primitive vertebrate. It has been suggested that cartilage developed as an embryonic tissue ; if this is so either the skeleton of the dogfish represents the original vertebrate embryonic skeleton, or its resemblances to the embryonic skeleton of higher vertebrates are due to convergence.

CLASS II—OSTEICHTHYES OR ACTINOPTERYGII

These are the bony fishes in the ordinary sense of the term. Their characters are in general the opposite of those of the

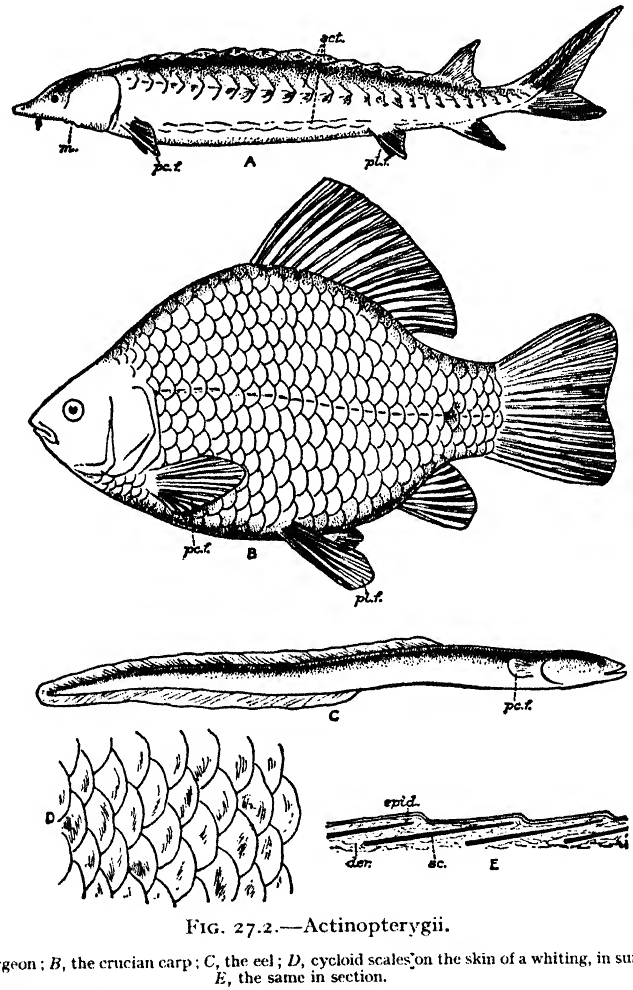


FIG. 27.2.—Actinopterygii.

A, The sturgeon ; *B*, the crucian carp ; *C*, the eel ; *D*, cycloid scales on the skin of a whiting, in surface view ; *E*, the same in section.

der., Dermis ; *epid.*, epidermis ; *m.*, mouth ; *pc.f.*, pectoral fins ; *pl.f.*, pelvic fins ; *sc.*, scales ; *sct.*, bony plates or scutes.

Chondrichthyes. The endoskeleton is bony throughout, but there are no placoid scales ; the gills are produced into long filaments and the gill slits are covered by an operculum ; an air bladder is present, but it does not function as a lung ; there are no claspers ;

and they lay large numbers of small eggs. There are three primitive orders, mainly extinct but including the modern sturgeons (*Acipenser*) and some others, which share, in varying degrees, the elasmobranch characters of muscular conus, spiracle, heterocercal tail, and spiral valve. The fourth order, the Teleostei, which includes the vast majority of fishes, including nearly all those familiar in British waters, such as the trout (*Salmo trutta*) and cod (*Gadus callarias* = *G. morrhua*), differs from the Chondrichthyes in these points also. The tail of teleosts is homocercal (Fig. 27.3), that is, it is externally symmetrical but goes through an asymmetrical stage in the embryo and may retain internal vestiges of this. Alone amongst the lower vertebrates, the teleosts have no cloaca.

CLASS III—CHOANICHTHYES (=CROSSOPTERYGII=SARCOPTERYGII)

Neoceratodus, *Lepidosiren* and *Protopterus* are the lung-fishes of Queensland, South America and Africa respectively; their air-bladders (one in *Neoceratodus*, a pair in each of the others) function

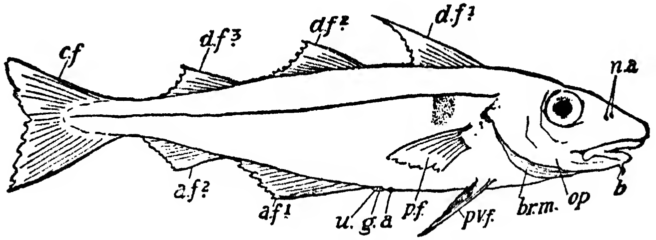


FIG. 27.3.—A diagram of the haddock.—From Thomson.

a., Anus; *af*.1, *af*.2, anal fins; *b.*, barbule; *br.m.*, branchiostegal membrane (a continuation of the gill cover); *cf.*, caudal fin; *df.*1–*df.*3, dorsal fins; *g.*, genital opening; *na.*, nasal openings (double on each side); *op.*, operculum or gill cover; *pf.*, pectoral fin; *pvf.*, pelvic fin; *u.*, urinary opening.

as lungs, and to fit this use there is a special blood supply, and there are internal nares. All three are tropical and live in water which must often be poor in oxygen. *Lepidosiren* and *Protopterus* normally survive the season when the rivers in which they live dry up, by resting in the mud. The lung-fishes are known as Dipnoi, and are associated with other extinct forms as the Choanichthyes. They are very important in any discussion of the origin of land vertebrates, but as the elementary student is never likely to meet them we shall not consider them in detail here. In general, apart from the possession of lungs,

their characters are primitive and elasmobranch-like, and in two respects they are even more primitive than the cartilaginous fishes; the gut of the modern Dipnoi is ciliated, and there are no vertebræ, the notochord being persistent. The Choanichthyes were well established in the Devonian period. A living form, *Latimeria* (Fig. 30.5), which closely resembles the extinct species, has recently been discovered in African waters.

Some authors associate the Crossopterygii and Actinopterygii as sub-classes of a single class Osteichthyes.

Tetrapoda

The rest of the vertebrates, called the Tetrapoda, or four-footed creatures, agree in being air-breathing and in having pentadactyl limbs. As we shall see later the adjective 'pentadactyl' is not to be taken too literally; it describes a typical condition, in which there are five fingers (or toes) but is used also for any limb which is built on the same general plan, however much it may be reduced. A few tetrapods have so little trace of limb-skeleton that one cannot credit them with possessing even vestiges of pentadactyl limbs, but their other features associate them with animals which are clearly not fish. Tetrapods also differ from all the earlier classes in that if they have unpaired fins these never contain skeletal rays; in the possession of a tympanic cavity in the ear; and in the possession of a cloacal bladder for storing waste products.

CLASS IV—AMPHIBIA

The modern amphibians are adequately characterised by the possession of a tadpole larva with functional gills; this metamorphoses into an air-breathing adult which retains some primitive and fish-like features, such as a long conus arteriosus, symmetrical arterial arches and a mesonephric kidney (p. 627). Many of the extinct forms are difficult to separate on the one hand from Choanichthyes and on the other from reptiles, but show a primitive type of skeleton such as one might expect in

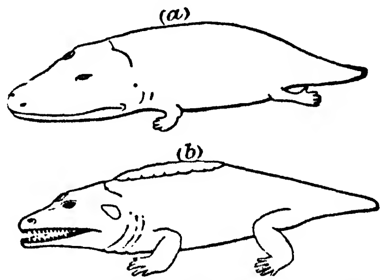


FIG. 27.4.—Stegocephalia.—From Swinnerton.

(a) *Mastodonsaurus* (Upper Trias); (b) *Cacops* (Permian).

an animal which was beginning to walk on land. The early amphibians, found first in Devonian rocks, are placed in the sub-class Stegocephalia. They were mostly large, up to seventeen or eighteen feet long, but with small limbs that could not have done more than push the body clumsily over the ground. The

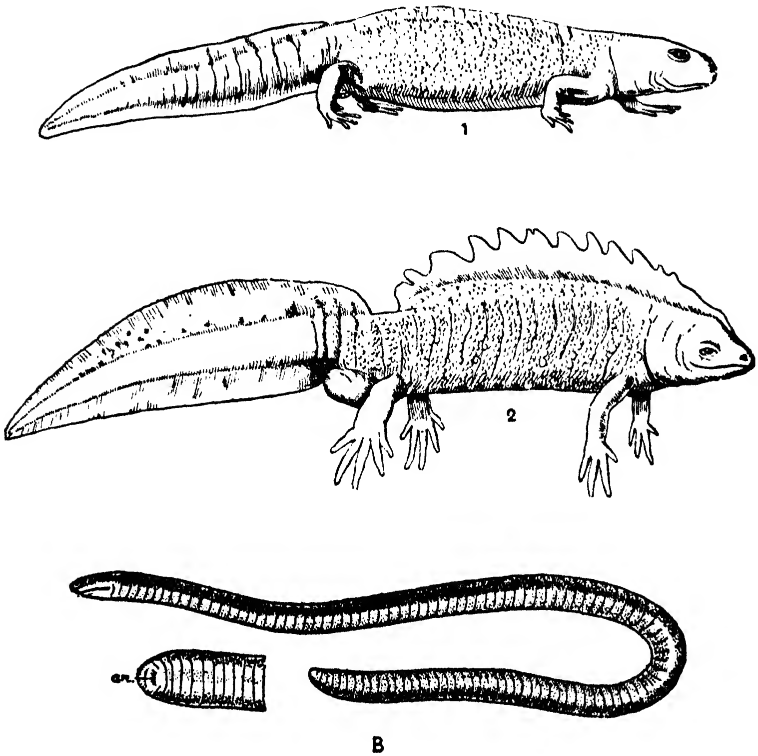


Fig. 27.5.—Amphibians.

A, The warty newt (*Molge cristata*); 1, female; 2, male at the breeding season, showing the crest which is specially developed at that time; *B*, *Cœcilia*, one of the Gymnophiona. *an.*, anus, in an enlarged view of the underside of the hinder end. Note the absence of a tail.

skull contained a large number of bones, and in some the body was armoured. Although they were, so far as is known, the earliest land animals, the chance of their having given rise to any existing descendants seems remote. The modern species of Amphibia, which have few ancient relatives and no known ancestry, are placed in three sub-classes. The Urodela retain the tail in the adult, have small limbs, and although air-breathing are largely aquatic. There are three species of newt, *Triturus* (=*Molge*

=*Triton*) in the British Isles; the salamander (*Salamandra*) of Europe, and the mud-puppy (*Necturus*) of North America are commonly dissected. On land they walk on their limbs, in water they swim in a fish-like manner, most of the propulsion presumably coming from the compressed tail, but while some species are mainly terrestrial, others are entirely aquatic. The Anura are a highly aberrant sub-class and have probably been separated from the urodeles since very early times. The tail is lost, the hind limbs are elongated, and there are many changes, mainly in the direction of loss or reduction, in the skeleton. The frog is an example, and there are also to be found in Great Britain a few individuals of the edible frog, *Rana esculenta* (mainly in East Anglia) and two species of toad, *Bufo bufo*, the common toad, and *B. calamita*, the natterjack. Both Anura and Urodela have skins which are unprotected by scales. The members of the last sub-class, the Gymnophiona (=Apoda), have lost tail, girdles and limbs, but have small scales in the dermis. The embryos are not free-living. Most of the adults are terrestrial and burrowing; there are no British species.

AMNIOTA

The remaining three classes of vertebrates are all primarily land-living, and all air-breathing whatever their habitat. Their embryos use as a respiratory and excretory organ the allantois, an outgrowth from the hind gut apparently homologous with the cloacal bladder of Amphibia. There is also another outgrowth from the embryo, a double fold of tissue called the amnion, which is presumably protective. The kidney is a metanephros. They are collectively called Amniota.

CLASS V—REPTILIA

The reptiles can only be characterised as amniotes which are not mammals or birds. Their skeleton and their circulatory system show various degrees of development towards the avian or mammalian condition; thus the ventricle of the heart shows a complete range of subdivision from the lizard, in which it is single as in the frog, to the crocodile in which it is completely divided by a septum except for a small foramen. Both systemic arches are present, but one is usually reduced. A complete scaly covering is almost universal, and all reptiles are cold-blooded.

They are divided into a number of main groups by the structure of the skull, as described later in this Chapter (p. 583) and again into several orders. The only orders with extant species are the Chelonia (tortoises and turtles), the Rhynchocephalia (containing only *Sphenodon* from New Zealand), the Squamata (lizards and snakes), and the Crocodilia. Great Britain has only six species, all Squamata. *Lacerta vivipara* is the common lizard, *L. agilis*, the sand lizard, which is of very local occurrence, and *Anguis fragilis*, the slow- or blind- worm, which is legless and snake-like ; there are also three snakes, *Vipera berus*, the adder, *Natrix natrix*, the grass snake, and *Coronella austriaca*, the smooth snake which is rare and local. Contrary to popular belief Ireland is not free from reptiles, for the common lizard is found there.

CLASS VI—AVES

The birds are warm-blooded, flying amniotes with feathers. Except for some extinct forms they have lost their teeth, but in the skeleton and soft parts generally they differ little from reptiles. There are scales on the legs, the circulation is reptilian, and they lay large yolky eggs, which are, however, much more cleidoic, or shut off from the environment, than those of reptiles. There are a number of adaptive features connected with flight, and a great development of instincts, such as those of migration, territory holding, nest-building and song, which are ancillary to reproduction. The classification of birds is difficult, partly because they are so uniform and partly for lack of fossils. Most of the birds of the world, and all the British species, belong to the super-order Neognathæ. The remainder, the penguins, ostriches and some others, are all flightless, but most are not closely related. The ostriches and similar running birds (the former Ratitæ) are now by some authors included in the Neognathæ.

CLASS VII—MAMMALIA

The mammals have already been considered in Chapter 25.

STRUCTURE AND EVOLUTION OF VERTEBRATES

The types which we have considered in earlier chapters fall fairly easily into a rough series, the members of which show increasing complexity. The earliest chordate was probably a

small filter-feeding organism of sluggish habits, which, were it alive to-day, might be put in the same sub-phylum as *Balanoglossus*. The relationships of these creatures to invertebrates are obscure ; the books which have been written to demonstrate that the chordates are derived from annelids or arthropods contain more invention than sense, and are chiefly interesting as showing what the human mind can be made to believe when there is no evidence. There are some similarities of embryology between the chordates and the echinoderms, and also some points of biochemistry in which they resemble each other and differ from most other invertebrates. The only theory then which has any support is that the chordate and echinoderm phyla once had a common ancestor, but it is unlikely that it was much above the cœlenterate level.

The next stage in chordate evolution was probably the acquisition of the postanal tail, and with it went a change in habits to a more active life ; *Branchiostoma* and the ascidian tadpoles are modern representatives of this level of organisation. Thus far the chordates were marine, but at some time in the Ordovician era they seem to have become ' fish ' in the general sense of the term. The earliest fossils of this type of which we know anything are the ostracoderms of the Ordovician, and these and the pteraspids, cephalaspids and anaspids of the Silurian periods ; they have all the main vertebrate features (so far as these are capable of being preserved in the rocks) except the jaws, and are a long way from the lancelet. We must suppose that there is a long unknown history, during which the vertebrate skeleton and other characteristics were evolved. With the acquisition of jaws the Agnatha developed into some sort of bony fish, the earliest known fossils being the acanthodians of the Silurian. After this, evolution took two courses. Some fish stayed in the sea and became the modern elasmobranchs while the others entered fresh water and developed into the ' bony fishes '. Some of these returned to the sea as Actinopterygii, while others, the Choanichthyes, remained in the Devonian lakes and developed lungs as an auxiliary method of breathing. The most successful of them crept out into the air and became Amphibia, and some of these abandoned the water altogether and became reptiles. From the reptiles a much later bifurcation gave rise to the birds and mammals. We shall now trace the development of the main organ systems along these lines.

THE TAIL

The general shape of the original vertebrate was presumably that of a fish, and it swam in the water in which it lived chiefly by means of unpaired fins. These were supported by rods of bone or cartilage, and in addition by 'fin rays' of varied chemical nature. The most important of these unpaired fins is the caudal, which surrounds the tail in a vertical plane; it has a number of

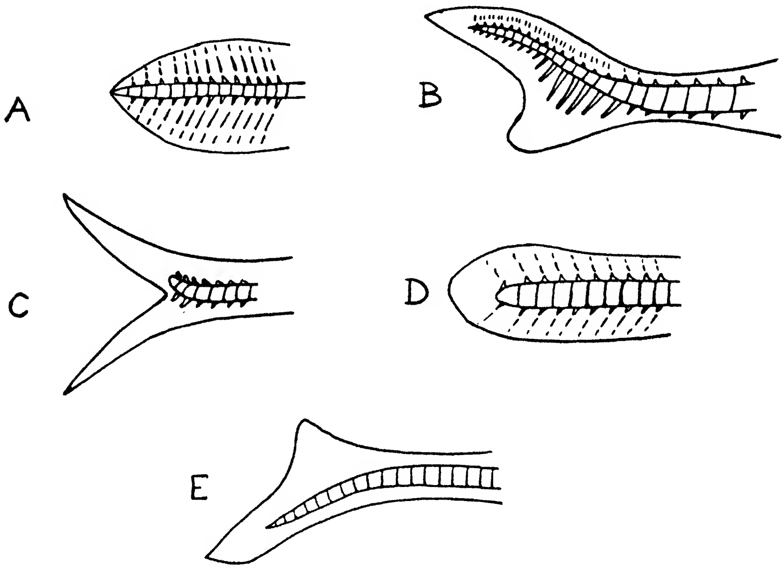


FIG. 27.6.—Diagrams of tails of fishes. The neural and hæmal spines, the radials and dermal fin-rays, which variously support the caudal fin, are not shown.

A, Hypothetical protocercal type; *B*, sturgeon, heterocercal type; *C*, herring, homocercal type; *D*, lamprey, diphycercal type; *E*, *Birkenia*, hypocercal type, of which the details are unknown.

different forms, both internal and external, and these are classified into five main types.

One would expect the earliest caudal fin to be symmetrical, with the vertebral (or notochordal) axis running straight to its tip, and with two equal expansions of membrane, one above and one below, but such a tail is found neither in any early vertebrate nor in any existing fish. It is, however, found in *Branchiostoma*, in early fish embryos, and in the larvæ of Amphibia. It is called protocercal (Fig. 27.6).

The oldest vertebrates had caudal fins which were strongly asymmetrical. In the Placodermi, in the earliest elasmobranchs,

and in the earliest bony fishes the vertebral column turns sharply upwards, a condition called heterocercal. The hæmal spines and rays which support the lower part of the fin are elongated, so that it is morphologically true to say, as is often done, that the lower lobe of the tail is larger; this is, however, somewhat misleading, as when the tail is looked at from outside, without dissection, the appearance may be that of a large upper lobe containing the vertebral column, with a smaller ventral lobe supported only by spines and rays, as one sees it in the dogfish. In other fish, as in the extinct shark *Cladoselache*, the two lobes appear of equal size. Heterocercy is found in nearly all elasmobranchs, and in sturgeons. The other type of asymmetrical caudal fin, called hypocercal, or reversed heterocercal, is found in the early Agnatha (ostracoderms). It is a mirror image of the heterocercal type; the vertebral axis turns downward and the neural spines or their radials are elongated. It is found in no living forms.

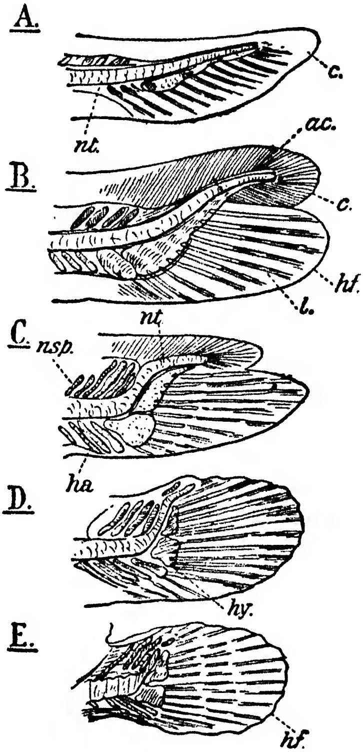


FIG. 27.7.—Stages in the development of the homocercal tail of the flounder (*Pleuronectes flesus*). From Goodrich, *Studies on the Structure and Development of Vertebrates*, 1930. Macmillan, London. After Agassiz.

ac., Actinotrichia; *c.*, axial lobe; *ha.*, hæmal arch; *hf.*, hypochordal fin; *hy.*, hypural cartilage; *l.*, dermal ray; *nsp.*, neural spine; *nt.*, notochord.

The two other types of tail are both externally symmetrical, but show signs, in internal structure, in embryology, in fossil history, or in more than one of these, of a former asymmetry. If the symmetry is now complete, both internally and externally, the fin is called diphycercal; such is the condition in the lamprey and in the living lung-fishes. The development of the tail of the lamprey shows signs of a hypocercal condition, as would be expected. The last type, the homocercal, has an internal structure

suggesting a heterocercal origin, as the notochordal axis is slightly upturned and much shortened, so that the fin is supported almost entirely by the rays. This condition is typical of the teleosts, and its development through the heterocercal state can be followed in embryology (Fig. 27.7).

When the fishes left the water and became tetrapods the unpaired fins were lost. Substitutes have, however, been acquired by nearly all the vertebrates which have returned to a fully aquatic existence; these include the Ichthyosauria amongst reptiles and the whales amongst mammals. In the whales the caudal fin is flattened horizontally instead of vertically, but cinema photographs have shown that, except for this difference, the method of swimming is similar to that of the fish. In none of these secondarily acquired unpaired fins are fin-rays present.

PAIRED LIMBS

The structure of the paired fins of fish is generally similar to that of the unpaired fins; there are proximal bony skeletal elements and distal rays, both surfaces are covered with muscle, and the whole is covered with skin. This similarity suggests a similar origin, and it is reasonable to suggest that just as the unpaired fins other than the caudal developed as devices to prevent rolling, so the lateral fins developed to prevent pitching. To make things appear neater it has further been suggested that originally the lateral fins, like the dorsal and ventral ones, ran most or all the length of the body. This 'lateral fin fold theory' has a small amount of fossil support in that the early sharks *Cladoselache* and *Diademodus*, and the agnathan *Cephalaspis* appear to have had fins which merge gradually into the body fore and aft, and so look like restricted portions of a continuous fold. Some early sharks have more than two pairs of fins; *Climatius*, for example, has seven (Fig. 27.8). It is possible that only the pectoral fins were derived from the fin-fold, and that the pelvic fins were independently evolved as copulatory organs, since that is almost their sole function in the dogfish.

The details of the fin skeleton of early fishes vary rather widely, and it is difficult to take any one arrangement as an ancestral or central type. The student will not be greatly misled if he takes the familiar arrangement of the dogfish pectoral fin (Fig. 21.6) as a starting-point; there are three large basals, several radials

distal to this, then polygonal plates, and finally the horny rays supporting the skinny part of the fin. The pelvic fin is a variant of this with a single basal, and other sharks have other numbers. In the modern actinopterygians there is only one set of bony elements, probably radials, and these have sunk into the body-wall so that the rays make the sole external support for the fins.

All such fish-fins are included in the general term ichthyopterygium, and from this is derived the cheiropterygium of the tetrapods, a generalised diagram of which is shown in Fig. 24.1. There is no direct fossil evidence of the change-over, but it is not unreasonable to believe that the basals became the

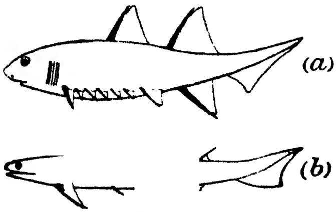


FIG. 27.8.—Placoderm fishes.—From Swinnerton.

(a) *Climatius* (Devonian) ; (b) *Acanthodes* (Permian).

Both belong to the Order Acanthodii, which had a strong spine in front of each fin. *Climatius*, one of the oldest known fishes, has on each side a row of small fins from the pectoral to the pelvic.

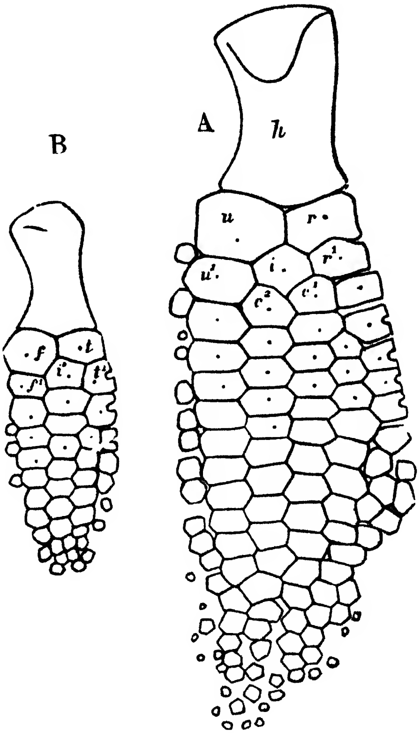


FIG. 27.9.—Right forelimb (A) and hind-limb (B) of Ichthyosaur.—After Lydekker.—*Guide to Fossil Birds, Reptiles, etc.*, British Museum (Natural History), 1934.

c^1, c^2, Centrale ; *f*., fibula ; f^1., fibulare ; *h*., humerus ; *i*., intermedium ; *r*., radius ; r^1., radiale ; *t*., tibia ; t^1., tibiale ; *u*., ulna ; u^1., ulnare.

humerus or femur, and the radials the other bones. In the nomenclature of those which form the wrist and ankle there is unfortunately much confusion, human anatomists favouring one set of names and zoologists another ; the chief variants are shown in Table VII. The primitive number of digits is probably five in each limb, but there are no modern Amphibia and few Stegocephalia with the full set of twenty. The hind-limb of the frog is specialised for both jumping and swimming, and has very long tibiale and

fibulare. Both limbs show a feature of no obvious adaptive significance, which is found also in many other vertebrates—the fusion of tibia and fibula and radius and ulna. Except where, as in the forearm of man, they can be rotated on one another, there is presumably no advantage in having two bones in this position.

The reptiles show a wide range of limb structure, including types which are primitive and others which are highly specialised

TABLE VII.

Nomenclature of bones of wrist and ankle, preaxial border on left. The names recommended for zoological use are in the top line in each row ; where the names recommended by the Anatomical Society of Great Britain differ from these, they are in the second line. Names in the third line are best avoided.

Proximal Row	Carpus	Radiale	Intermedium	Ulnare	
		Scaphoid	Lunate	Triquetral	
			Lunar	Cuneiform	
	Tarsus	Tibiale		Fibulare	
		Talus		Calcaneum	
		Astragalus			
Middle Row	Carpus	Centralia, numbered from preaxial border			
	Tarsus	Centralia, numbered from preaxial border			
		In man, navicular			
Distal Row	Carpus	Trapezium	Trapezoid	Magnum	Unciform 1, 2
				Capitate	Hamate
	Tarsus	Ento-cuneiform	Meso-cuneiform	Ecto-cuneiform	Cuboid
		Medial, intermediate and lateral cuneiform.			

(Figs. 27.9, 27.10). The snakes have no limbs at all, but a few have small, functionless femurs which do not project beyond the body-wall. Limbless lizards, such as the slow-worm (*Anguis fragilis*) of Britain, are also without limb skeletons. The structure of the wing of a bird (Figs. 23.9, 23.14) is primitive in that both ulna and radius are separate bones and unspecialised in form, but the wrist and hand are much modified. The reduction of the digits is presumably connected with flight, as only one finger is needed to support the main feathers, but the peculiar fusion of the metacarpals with the distal carpals seems to be merely a peculiarity of no functional importance. It is paralleled in the hind-limb (Fig. 23.14), and was probably found also in the bipedal dinosaurs.

The limbs of mammals show an extraordinary diversity, and illustrate better than almost any other structure the principle of adaptive radiation by which one basic plan becomes modified to fit different habits and habitats. A primitive type is found in a

plantigrade insectivore such as a hedgehog, although even here there are specialisations such as the loss of the centrale (present in the mole) and the fusion of radiale and intermedium. The commonest type of development is an elongation of the hands and feet, so that the animal walks on the phalanges of its digits

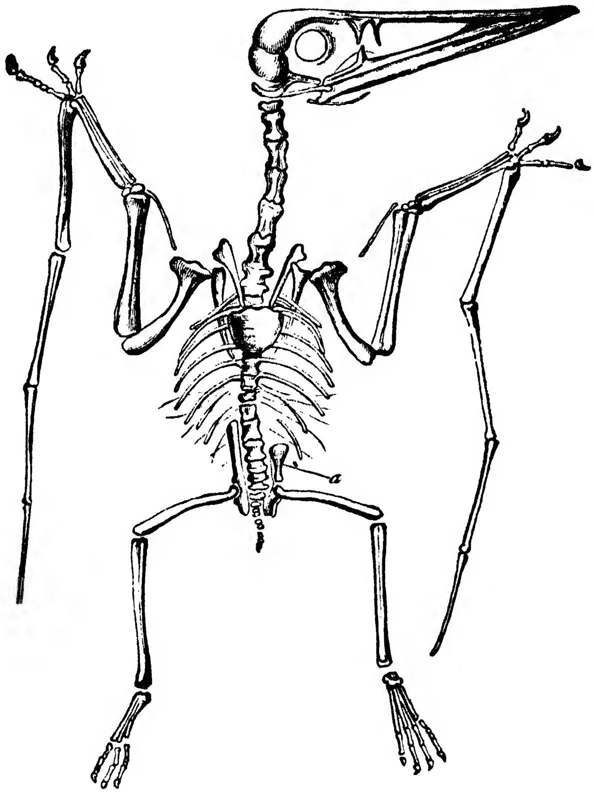


FIG. 27.10.—Skeleton of pterodactyl. × 1. *Guide to Fossil Birds, Reptiles, etc.*, British Museum (Natural History), 1934.

(*a*) Pubic bone.

(digitigrade) or on the nails at their tips (unguligrade). The rabbit (Fig. 24.5) is a rather bad example of a digitigrade animal, the cat or dog (Fig. 27.11) is a better one. The limbs are capable of little movement except in the fore and aft plane, so that there is a tendency for fusion of the bones of forearm and shank, and for the development of pulley-like joints. The chief unguligrade mammals are the artiodactyls and perissodactyls, which show a reduction of digits which is achieved in different ways in the two

orders. The horses and some cattle (Figs. 25.10, 25.11, 25.15, 25.16) show the limit of reduction by the two methods. Other artiodactyls, such as the hippopotamus, have four toes, other perissodactyls, such as the rhinoceroses, have three, but whatever the number the axis goes down the third digit in the perissodactyls and between the third and fourth in the artiodactyls. In the graviportal or very heavy mammals such as the elephant, the proximal bones of the limbs, humerus and femur, are longer than the others.

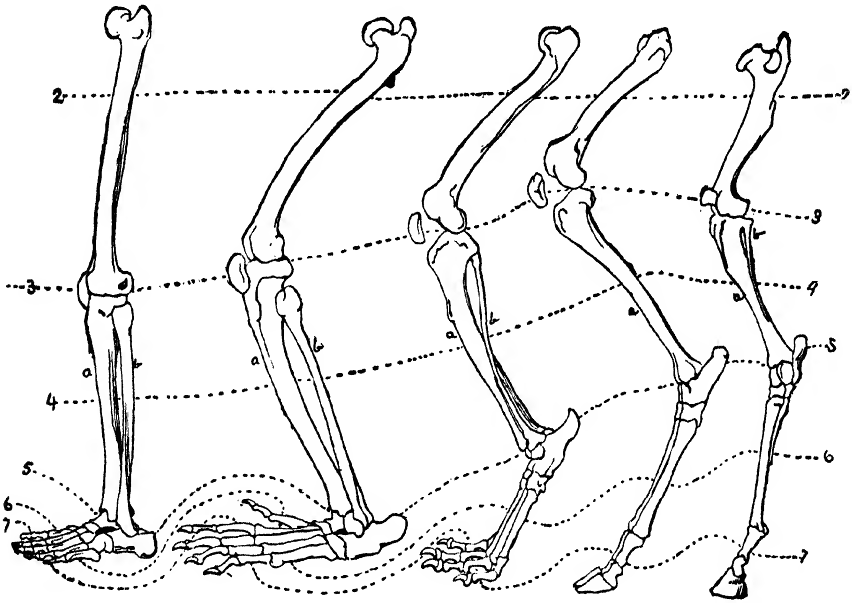


FIG. 27.11.—The bones of the hind-limb of Man, compared with those of a monkey, dog, sheep, and horse. Homologous parts bear the same letters or numbers. —From Romanes, after Le Conte.

The advantage of the digitigrade and unguligrade conditions is that they allow the animal to move faster, and so they are found in the cursorial forms, which run either to catch their prey or to avoid being caught. There is a general tendency in such species for the hind-limbs to do more than half the work of propulsion, and this leads, as in the rabbit or dog, to an increased relative size of their muscles and the bones to which they are attached. The extreme of this is seen in the saltatorial or jumping animals in which the fore-limbs are not used in locomotion at all. The kangaroos are the best known examples, but a similar condition is found in three families of rodents. It is notable that where-

as all but the smallest birds use their legs alternately, the only bipedal mammal which does so is man. In walking his hind-limbs are plantigrade, but his peculiar foot allows digitigrade running (Fig. 27.11). His fore-limbs (Fig. 24.20) are remarkable for opposability of the thumb and for the degree of twisting of which the forearm is capable. These features, perhaps originally useful for climbing trees, are generally considered to have assisted in the development of man's brain by allowing him to grasp and inspect solid objects, and so to have more to think about. The only vertebrates except the primates which can handle things in a comparable way are some rodents, notably the squirrel, and a few birds, especially the parrots. The last have much larger cerebral hemispheres in proportion to their size than any other birds.

Extreme modification of limb structure is found, as would be expected, in those mammals which have ceased to walk on the surface of the land. In the toothed whales there is no trace of any skeleton of the hind-limb, and in the whalebone whales there are only small internal bones representing at most femur and tibia. The fore-limb in both groups has become a flattened paddle, with no external trace of digits. The bones are reduced in length, and packed tightly together, so that there is some resemblance to the condition in the dogfish (Fig. 25.8). There is much irregularity in the arrangement of the carpals, and their homology is difficult. Hyperphalangy—an increase in the number of phalanges above the normal—is usual. In the bats the whole fore-limb is lengthened, and the wing is supported chiefly by the middle phalanges of digits I, III, IV, and V in the fruit-eating bats, or the metacarpals of II to V in the insect-eating forms (Fig. 30.8). The ulna is almost lost. The hind-limbs are short, and only the digits are free.

LIMB GIRDLES

The proximal bone of each limb articulates with a special inner part of the skeleton, called a girdle, pectoral for the fore-limb and pelvic for the hind. These girdles are generally considered to be derived from the anterior basals of the protovertebrate fins, which have sunk inwards and become enlarged. In addition, in the pectoral girdle only there may be a superficial series of dermal bones, which are probably only secondarily associated with the limbs. In fishes, the endoskeletal girdle is usually relatively simple ; there is a single cartilage or bone, or sometimes

two or three, on each side, and no sort of attachment to the vertebral column. In the dogfish (Figs. 21.6, 21.7) the cartilages of each side meet and fuse ventrally in both girdles. The names given to the portions of the girdles, or to their separate elements, are descriptive only, and must not be taken to imply homology. The modern elasmobranchs have lost all trace of exoskeleton except in so far as the dermal denticles are homologous with the armour of the early vertebrates (see p. 550), but the bony fishes have not only a series of superficial bones in the skull, but a dermal shoulder girdle as well. It is attached dorsally to the temporal region of the skull, and runs down in a half-hoop behind the gill slits; its functional importance is that where the gill slits are large and placed close together the body-wall in the pharyngeal region is very much weakened. The dermal girdle then fastens the head to the rest of the body. It is seen at about its maximum in the primitive actinopterygian *Polypterus*. The only bone not present here is the interclavicle, a median ventral piece which often unites the clavicles of the two sides. In the teleosts (Fig. 27.12) the cleithra meet ventrally and the clavicles are generally absent.

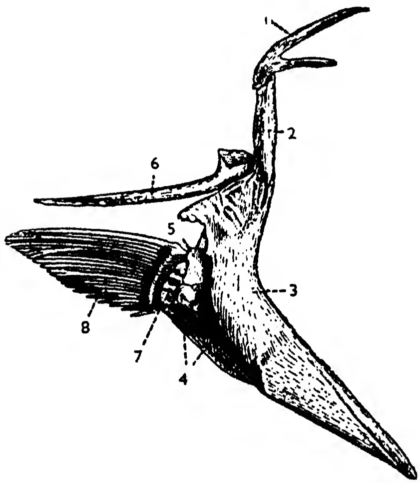


FIG. 27.12.—The right half of the pectoral girdle and right pectoral fin of a cod.—From Reynolds.

1, Post-temporal; 2, supracleithrum; 3, cleithrum; 4, coracoid; 5, scapula; 6, post-cleithrum; 7, brachial ossicles; 8, dermal fin rays.

In swimming animals the girdles are mere articulating points on which the fins can be turned in their functioning as elevators, but in land animals they come more and more to bear the creature's weight as the body is lifted off the ground. In consequence they become progressively strengthened and more firmly attached to the backbone. The change, however, is a gradual one. A young newt when put on land uses the muscles all the way down the body, and throws its whole length into waves similar to those seen in a swimming fish. It is probable that the earliest Stegocephalia did no better; their heavy bodies

were dragged over the land, and their shoulder girdle was entirely fish-like, with a post-temporal connection to the skull (Fig. 27.13). By contrast the urodeles have lost the whole of the dermal girdle and the Anura retain only the clavicle. In its shoulder girdle, as in other parts of the skeleton, the frog retains much cartilage; its endoskeletal part has two ossifications, called scapula and coracoid, but, for reasons which will appear below, the cartilaginous part should not be called precoracoid.

Nearly all tetrapods show three

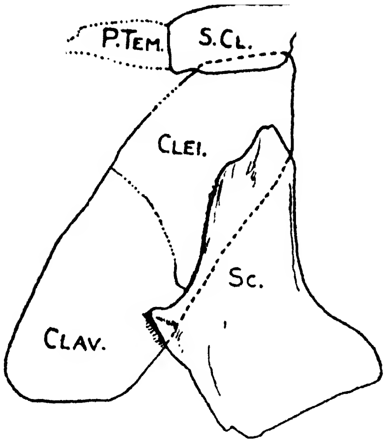


Fig. 27.13.—Shoulder girdle of a stegocephalian, *Eogyrinus*. Right half, inner surface.—From Watson, 1926, *Phil. Trans. B*, 214, 189.

Clav., clavicle; Clei., cleithrum; P.Tem., post-temporal; Sc., scapula; S.Cl., supracleithrum.

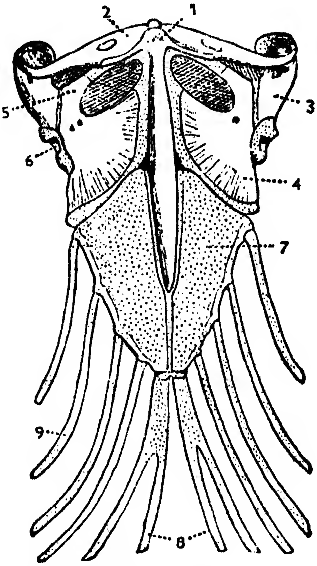


Fig. 27.14.—A ventral view of the shoulder girdle and sternum of *Loemanctus longipes*, a lizard.—From Shipley and MacBride.

1, Interclavicle; 2, clavicle; 3, scapula; 4, coracoid; 5, precoracoid; 6, glenoid cavity; 7, sternum; 8, sternal bands; 9, sternal portion of a rib. The dotted regions are cartilage.

distinct bones in the pelvic girdle, which is entirely endoskeletal and is preformed in cartilage. These are the dorsal ilium, anteroventral pubis, and posteroventral ischium. It would be satisfactory to be able to homologise the pectoral girdle to this plan, but unfortunately modern tetrapods have not more than two cartilage bones in the shoulder. There are, however, some extinct reptiles and some Stegocephalia which have two ventral elements, and it is now generally believed that the primitive tetrapod shoulder girdle consisted of a dorsal scapula, an anteroventral precoracoid, and a posteroventral

coracoid. In modern forms it is sometimes the coracoid and sometimes the precoracoid which is missing, but as the names were given to the bones before the original tripartite division was known, any ventral element is usually called coracoid, irrespective of which bone it represents. The three bones in each girdle all contribute to the articular surface for the limb—glenoid in the shoulder and acetabulum in the hip.

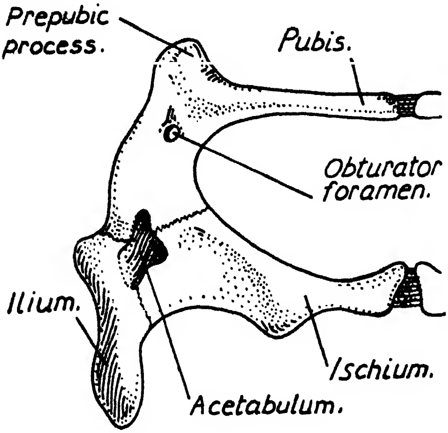


Fig. 27.15.—Right half of pelvic girdle of lizard (*Uromastix*) in ventral view.

The ventral element in the frog's shoulder girdle is a precoracoid. By contrast the pubis remains cartilaginous, but the most striking thing in the pelvic girdle is the great length of the ilia which stretch forward to join the ninth vertebra. Such a junction between hip girdle and backbone is called a sacrum. It is common

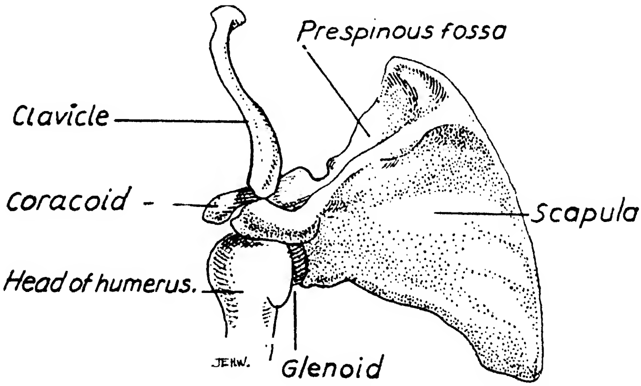


Fig. 27.16.—Shoulder girdle of man, from the side and slightly from the front.

for the pubes and ischia to meet in a ventral symphysis, but such a junction of the coracoids as occurs in the frog is unusual. The reptiles have various types of shoulder girdle, but in general in modern forms the scapula, precoracoid, clavicle, and interclavicle are well developed (Fig. 27.14). The same is true of the

birds, where the whole thing is firmly bound to the thorax by muscles. The scapula has a characteristic shape, and the pre-coracoids are large and meet the sternum ; they are thus able to resist the strong inward pull of the flight muscles (Fig. 23.9). Most reptiles have a pelvic girdle with all three bones of unspecialised type (Fig. 27.15). That of the birds (Fig. 23.9) is highly characteristic and is strengthened for bipedal gait by a well-developed sacrum. The pubes are turned backwards, and there is no ventral symphysis.

In mammals the scapula is enlarged and the coracoid reduced to a small bone which early in its development fuses with the scapula to form a process which is said to resemble the head of a crow, hence its name of coracoid. The clavicle is absent from or much reduced in running forms, but well developed in types such as man (Fig. 27.16) which can move their fore-limbs from side to side. The interclavicle is probably the bone usually called omosternum. All three bones are present in the pelvic region, but they fuse to form a single os innominatum.

POSITIONS OF LIMBS

In accordance with the fin-fold theory the primitive position of the paired limb was that of a flat plate projecting from the body ; it would then have a dorsal and a ventral surface, and a preaxial and a postaxial border, the axis here referred to being that of the limb itself. A human being lying prone (i.e. with face to the ground) will have his fore-limbs arranged in this position if he stretches his arms out at right angles to the body with palms to the ground. The palms are ventral, the radius and thumbs preaxial. In most fish the fins have rotated so that the ventral surface is posterior ; this can be demonstrated by turning the hands so that the thumbs are below. This is also the position in the primitive tetrapods. The later land animals, including many living reptiles, have raised their body by a double right-angled flexure of the limbs. Starting from the primitive position the upper arm remains in the same relation to the body, the forearm bends down until it becomes vertical, and the hand bends in the opposite direction at the wrist joint until its palm is again horizontal and in contact with the ground. In most mammals the humerus has rotated backwards and inwards so that the elbow is a backwardly directed joint, and the forearm and hand have rotated forwards and inwards to bring the radius

across the ulna and the thumb to the inside. The limb is then in the position adopted in the ordinary ' press-up ' of the gymnasium. The only common further development is a straightening of the limb so that in the standing position all the bones, from humerus to the terminal phalanges, run more or less in one line ; this is seen at its best in the horse or elephant.

The hind-limb goes through a similar series of changes, which cannot be illustrated in the human body. In the mammals, however, the femur rotates forward, not backwards like the humerus. The result of this is that while in both limbs the preaxial digit (thumb or big toe) comes to lie on the inside (medial in anatomical terminology), the preaxial border of the humerus is outside (lateral in anatomical terminology) and that of the femur is inside. Since also the rotation of the femur and that of the shank are in the same direction, the tibia does not have to cross over the fibula as the radius does over the ulna. As has been seen, the forearm of man retains much freedom of movement. In its primitive position, with radius and ulna parallel, it is said to be supine ; when they are crossed, to bring the thumb inside, it is said to be prone.

VERTEBRÆ

The segmentation of chordates is expressed chiefly in the mesoderm, and is seen at its simplest in the embryo of *Branchiostoma*, where the mesoderm develops as a series of paired pouches, each containing a part of the cœlom (Fig. 28.9). Ventrally the segmentation is lost, but each somite develops dorsally into the segmental muscle which is visible in the adult. In the embryos of vertebrates there is a similar, though often not so clear, arrangement of the somites, well seen in the second day chick. Each somite (Fig. 27.17) early divides into a number of parts, of which the chief are the myotome, which forms muscle, the nephrotome, which will be referred to below, and the sclerotome. In fishes the muscles retain their segmental arrangement, but in land animals, largely because of the new importance of the limbs and the rearrangement of the muscles which is necessary in order to work them, segmentation can only be made out in the embryo.

In all vertebrates the primary axial skeleton is the notochord, which is unsegmented, but it is always replaced more or less completely by the vertebral column. The development of this is

difficult to make out and it is not easy to homologise the parts in all groups. It appears, however, that the general arrangement

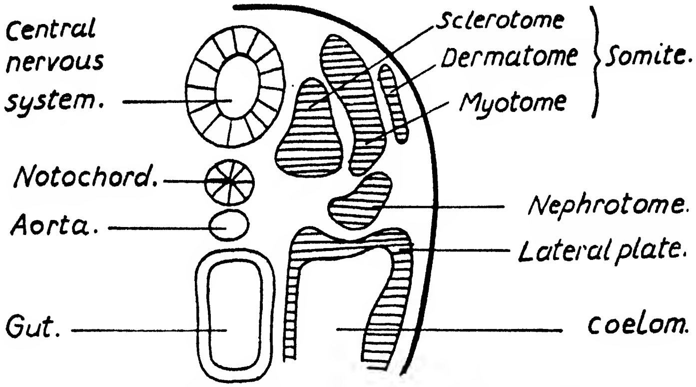


FIG. 27.17.—A diagrammatic transverse section of part of a mammalian embryo, showing the relations of the mesoderm.

is for the sclerotome of each side to divide into four, from which develop cartilages called arcualia ; these are the interdorsal and

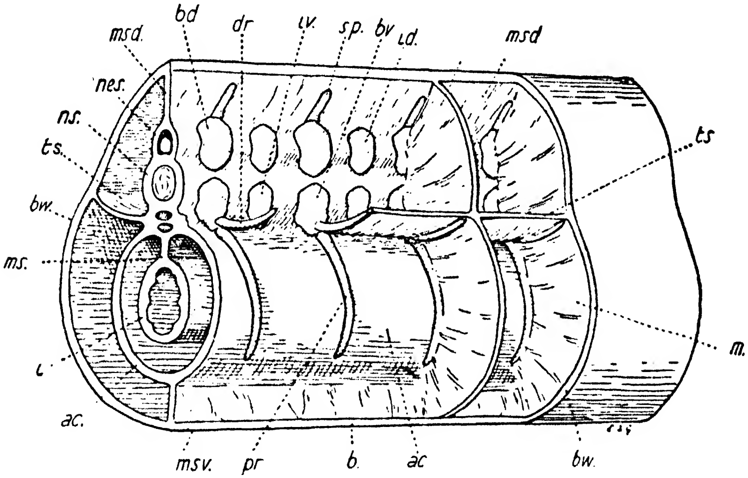


FIG. 27.18.—Diagram of the organisation of a vertebrate.—From Goodrich. Young, *The Life of Vertebrates*, 1950. Clarendon Press, Oxford.

ac., Wall of abdominal cœlom ; *bd.*, basidorsal : *bv.*, basiventral ; *b.* and *bw.*, body-wall ; *dr.*, dorsal rib ; *i.*, intestine ; *id.*, interdorsal ; *iv.*, interventral ; *m.*, myocomma ; *ms.*, mesentery ; *msd.*, median dorsal septum ; *msv.*, mediun ventral septum ; *nes.*, neural tube ; *ns.*, notochordal sheath ; *pr.*, ventral (pleural) rib ; *sp.*, neural spine ; *ts.*, horizontal septum.

interventral in front, and the basidorsal and basiventral behind (Fig. 27.18). The segmental muscle grows between the anterior and posterior pieces, so that the basals of segment *n* become associated

with the interdorsal and interventral of segment $n + 1$. The definitive vertebra is formed in various ways from the eight pieces which we have described (four on each side) but it is always

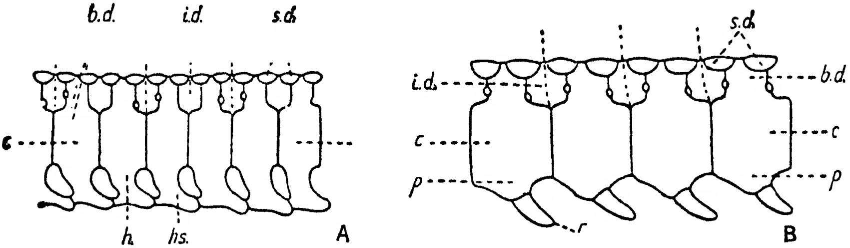


FIG. 27.19.—*A*, Trunk vertebræ of *Scyliorhinus canicula*, side view. *B*, similar view of caudal vertebræ.—From Young, *The Life of Vertebrates*, 1950. Clarendon Press, Oxford. After Ridewood.

b.d., Basidorsal; *c.*, centrum; *h.*, basiventral; *h.s.*, hæmal spine; *i.d.*, interdorsal; *p.*, pa apophysis; *r.*, rib; *s.d.*, supradorsal. The vertical dotted lines indicate the limits of the myotomes; the small circles represent the exits of the dorsal and ventral roots of the spinal nerves.

intersegmental in position. A great part of the centrum is also formed by an ossification in the unsegmented notochordal sheath.

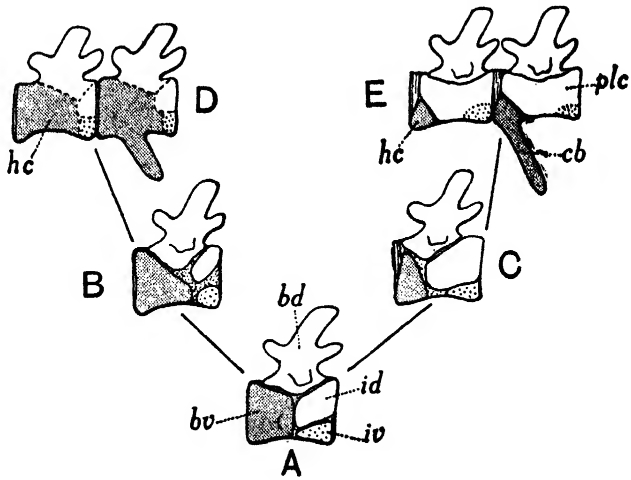


FIG. 27.20.—Diagram showing the probable evolution of the vertebræ of a typical amphibian, D, and a typical amniote, E. In D and E a caudal vertebra is shown as well as one from the trunk.—From Goodrich, *Studies on the Structure and Development of Vertebrates*, 1930. Macmillan, London.

bd., Basidorsal (neural arch); *bv.*, basiventral, which becomes *hc.*, hypocentrum; *cb.*, intercentrum; *id.*, interdorsal, which becomes *plc.*, pleurocentrum; *iv.*, interventral.

The arcualia are seldom visible in the adult, but traces of them may be seen in the dogfish, where the hæmal arch and lower part of the centrum represent the basiventral, the neural arch

represents the basidorsal, while the interdorsals and interventrals are the intercalary pieces, the latter being small. The supradorsals, generally miscalled neural spines, are extra cartilages (Fig. 27.19). In the Stegocephalia the arcualia, in various patterns, appear as separate bones. In the frog the vertebral column develops from largely unsegmented cartilages, but in the amniotes a fairly clear derivation from the arcualia can be made out, the neural arch being formed from the basidorsal, and the centrum mainly from the interdorsal (Fig. 27.20). Ribs are formed in the connective tissue between the muscle blocks, and so are intersegmental; their attachment, originally with the basiventrals, shifts in amniotes to the basidorsals and interdorsals.

The detailed form of tetrapod vertebræ has been adequately shown by the descriptions of those of the frog, pigeon, and rabbit. A peculiarity of amniotes is that the interdorsals of the first vertebra (atlas) fuse with the centrum of the second (axis) to form its odontoid process, while all that remains of the centrum of the atlas is formed from the basiventrals, which, with the neural arch (basidorsals) form a ring.

THE HEAD

If one considers the mammals alone, the definition of the head seems easy, but it is by no means certain that what is called the head in mammals is exactly homologous with the part of the body which bears the same name in birds or reptiles. Further, in amphibians and fishes where there is no neck it is not always very clear where the head ends and the trunk begins. We shall therefore, as is often the best way with biological terms, postpone any attempt at definition until we have considered some of the facts.

In the protochordates there is no head, but there is some degree of 'cephalisation', or development of the anterior end in the direction of a head. In *Branchiostoma*, for example, the segmentation runs fairly uniformly to the tip of the snout, but there are some specialisations in the mouth and anterior sense organs, and a slight enlargement of the central nervous system. In the dogfish, by contrast, there is a well-developed head with large sense organs, a skeleton which has no obvious resemblance to that of the trunk, and a complete absence of any visible trace of segmentation. Embryological investigations in the third quarter

of the nineteenth century showed, however, that the mesoblast of the head is originally segmented nearly to its tip, and that the obliteration of segmentation in the adult is merely the result of the development of the sense organs and of the formation of jaws. Further work has confirmed and extended this interpretation, but it is still not possible to give a fully satisfactory description of the cranium in terms of segmentation.

The embryology of the mesoblast described on page 665, and in Fig. 27.17, holds pretty generally throughout the vertebrates. The dorsal part is segmented, and each somite is early divided

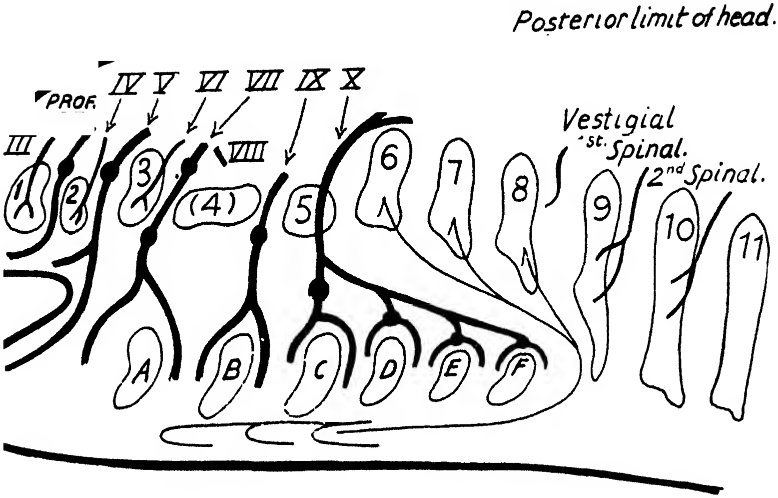


FIG. 27.21.—Diagram showing the segmentation of the head in a selachian.—Simplified from Goodrich.

A–F, Gill slits ; 1–11, somites ; III–X, cranial nerves.

into a myotome, forming muscles, and a sclerotome, forming skeletal elements. The main nerves are not themselves segmented, but since they emerge between the vertebræ and supply the muscles, they have a segmental arrangement impressed on them ; the ventral roots supply the myotomes, and the dorsal roots, chiefly but not entirely sensory, run behind the myotomes. The ventral part of the mesoblast remains unsegmented as the lateral plate. In the head of the embryo *Scyllium* a similar arrangement holds as far forward as the anterior end of the notochord—that is, to the level of the future hypophysis. In the region which will become the future head there are eight pairs of hollow somites, here called head cavities, which form

a continuous series with those of the body. The first is preoral, and the others correspond in position to the mandibular, hyoid, and five branchial arches. The lateral plate mesoblast contains a series of cavities which pass down these arches, which are formed when the gill slits pierce the body-wall intersegmentally. The spiracle is a non-functional gill slit anterior to the first, and the mouth appears to be formed by the confluence of two gill slits anterior to the spiracle. Part of the sclerotome grows down and helps to form the appropriate cartilaginous arch, though much of this comes from unsegmented mesenchyme derived from ectodermal cells of the neural crest. The connection of the sclerotomes with the dorsal part of the skull is not clear. The myotomes form the muscles of the eyeball, and each of these is supplied by the appropriate ventral root. The dorsal root passes behind the myotome and supplies the muscles of the jaw or branchial arches which have been formed from the lateral plate, and there is usually also a small pretrematic branch running to the segment in front. The dorsal and ventral roots of the cranial nerves thus remain separate throughout life, as the spinal roots do in *Branchiostoma* and *Petromyzon* ; in gnathostomes the spinal dorsal and ventral roots fuse. The segmental arrangement of the cranial nerves has no relation to their numbering as it is usually learnt by the student ; moreover, the optic and olfactory nerves are not strictly nerves at all, but extensions of the wall of the brain, and as such have no place in the scheme. The auditory nerve appears to be part of the facial which is specially developed in connection with the acustico-lateralis system of sense organs, of which the ear forms a part ; in the extinct cephalaspids, in the skulls of which the courses of the nerves can be traced, there was a complete series of segmental lateralis nerves. The spinal accessory of mammals is the last branch of the compound vagus in which it is elsewhere included. The blood vessels of the head correspond to the gills and are therefore segmental in position, but in the anterior region, where the gills are lost, there is some confusion.

The smooth arrangement of the head segments is disturbed in two ways. The preoral, mandibular and hyoid segments are disturbed ventrally by the development of the mouth and loss of the gills which may be presumed to have once been present, and the sense organs upset the dorsal part. The olfactory organ, being terminal, has little effect, but the eyes and ears are large and lateral, and leave little room for anything else in the segments

which they occupy. The eye occupies segments one, two, and three, the myotomes of which form its muscles, and the ear, with its containing skeletal capsule, occupies segment four so completely that its myotome is obliterated and disappears, and segment five so much that its myotome becomes vestigial. The remaining metotic myotomes contribute to the musculature of the epi- and hypobranchial regions.

A summary of the segmentation of the head is given in Table VIII. In some gnathostomes the number of metotic segments is different, both because the auditory capsule may obliterate more than two, and because a variable number is added in the occipital region. The primitive number of head segments is perhaps ten, which would correspond to seven pairs of gills, the number found in the shark *Heptanchus*. In Anura the ‘ head ’ is much shortened, as only five segments remain in the skull.

We can now consider what should be included in the term ‘ head ’. In the dogfish, and most other fishes, there is no difficulty ; there is a specialised anterior end of the body, containing dorsally the skull and brain and chief sense organs, and ventrally the mouth and gills, and although this is not divided physically from the trunk by any sort of constriction, it has been shown to correspond to a definite number of segments and there is no doubt where its posterior boundary lies. It may be defined shortly as that part of the body which is in front of the shoulder girdle. The importance of this girdle as the dividing line is seen very clearly in the teleosts, where it borders the last gill slit and is attached dorsally to the skull. In the tetrapods two difficulties occur. The first, that a variable number of segments takes part in the occipital region of the skull, has already been mentioned and need cause little confusion. The number of segments in different regions of the body of vertebrates is obviously highly variable, and no one is likely to try to define sacrum or fore-limbs, for example, in terms of the segments from which they are formed ; similarly we cannot expect to be able to define the head or the skull in this way. The second difficulty is greater. When the gill slits cease to be functional the ventral part of the head loses its importance, and can be suppressed or converted to other uses. In fact, part of the branchial skeleton and its musculature is transformed into the tongue and its supports, and remains within what is usually called the head, while the rest passes backwards so that it comes to lie beneath the anterior vertebræ

TABLE VIII.

The segmentation of the vertebrate head. The retractor bulbi is the muscle which in reptiles and mammals withdraws the eyeball, and the quadratus and pyramidalis move the nictitating membrane in birds.

Segment	Myotome	Skeleton	Nerve		Artery	Gill Slit
			Ventral	Dorsal		
1. Premandibular 1st Pro-otic	Rectus superior " inferior " anterior Obliquus inferior	Trabecula in embryo	Oculomotor	Deep Ophthalmic	Ophthalmic	Mouth
2. Mandibular 2nd Pro-otic	Obliquus superior	Polar cartilage in embryo Palatoquadrate Meckel's cartilage	Pathetic	Trigeminal	Mandibular or Spiracular	Spiracle
3. Hyoid 3rd Pro-otic	Rectus posterior (Retractor bulbi) (Quadratus and pyramidalis)	Parachordal in embryo Hyoid	Abducent	Facial and Auditory	1st branchial (Internal carotid)	1st gill slit
4. 1st Metotic	None	Parachordal in embryo 1st branchial arch	None	Glosso-pharyngeal	2nd branchial (Systemic)	2nd gill slit
5. 2nd Metotic	Vestigial	2nd branchial arch	Vestigial	Vagus	3rd branchial	3rd gill slit
6.–8. 3rd–5th Metotics	Epi- and hypo-branchial muscles	Occipital region of skull 3rd–5th branchial arches	Hypoglossal	Vagus Spinal Accessory	4th to 6th branchials (4 = pulmonary)	4th–5th gill slits

in what is functionally a new part of the body, the neck. The head of tetrapods thus corresponds only partially to that of fishes, and no formal morphological definition of the term 'head' seems possible which will satisfy the facts in all vertebrates.

THE CHONDROCRANIUM

In all vertebrate embryos a large part of the skull is preformed in cartilage, and in the Chondrichthyes the cartilaginous state persists; although it is probable that the absence of bone is secondary, the skull of the dogfish does represent fairly well

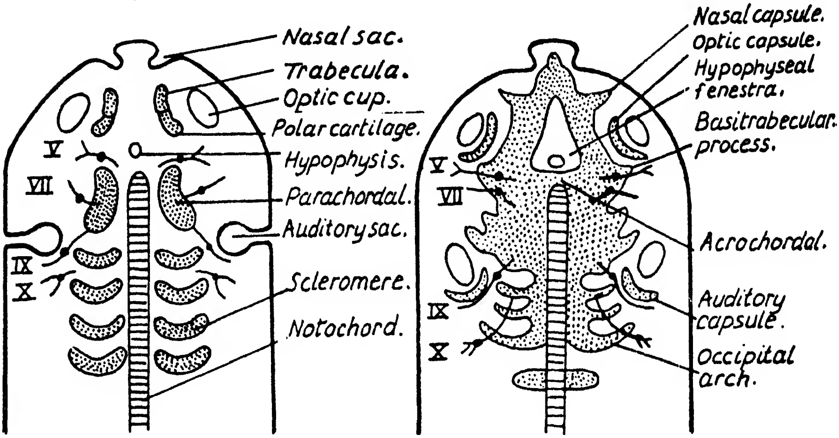


FIG. 27.22.—Diagrams showing the development of the chondrocranium in gnathostomes, dorsal view. Some cranial nerves are shown, on the right side only.—Simplified from Goodrich.

the chondrocranium, or cartilaginous skull, which may be presumed to have preceded in evolution the bony skull. A similar structure persists in modern Amphibia, although here a certain number of bones is added. Such a chondrocranium is seen to have an anterior ethmoid region, to the front of which is attached a pair of nasal capsules separated by a nasal septum; an orbitotemporal region more or less compressed to hold the eyes and having many foramina for the passage of nerves; an otic region, to which are applied laterally the paired auditory capsules; and a posterior occipital region with a more or less constricted exit, the foramen magnum, for the spinal cord. Together these partly enclose the brain, but this is exposed at places (the fontanelles) where the cartilage is incomplete (cf. Figs. 21.5 and 22.8). In the floor in the orbitotemporal region is the

hypophyseal fenestra, through which passes the hypophysis. When this becomes developed into the pituitary the fenestra may fill up, as in mammals, but its position is marked on the inside by a depression, the pituitary fossa, in which the gland lies. Up to the level of the fenestra or fossa the notochord extends beneath the skull. Beneath this are the jaws and other ventral elements of the skull, which will be considered later.

In early development the chondrocranium is made up from a number of separate cartilages (Fig. 27.22). Anteriorly the base

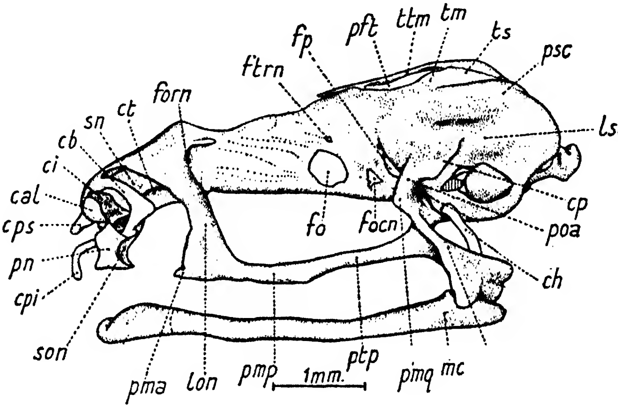


FIG. 27.23.—Cartilaginous skull of adult *Rana*.—From De Beer, *The Development of the Vertebrate Skull*, 1937. Clarendon Press, Oxford.

cal, *ci*, *cpi*, and *cps*, Nasal cartilage ; *cb*, ceratobranchial ; *ch*, ceratohyal ; *cp*, otic cartilage ; *ct*, trabecula ; *fo*, optic foramen ; *focn*, oculomotor foramen ; *forn*, orbitonasal foramen ; *fp*, pro-otic foramen ; *ftrn*, trochlear foramen ; *lon*, orbitonasal cartilage ; *lsc*, lateral semicircular canal ; *mc*, Meckel's cartilage ; *pft*, parietal fontanelle ; *pma* and *pmp*, maxillary process ; *pn*, nasal cartilage ; *poa*, adult otic process ; *psc*, posterior semicircular canal ; *ptp*, pterygoid process of quadrate ; *q* and *pmq*, quadrate ; *sn*, nasal septum ; *son*, nasal cartilage ; *ttm*, *ts*, and *tm*, roof of cranium.

of the cranium is made up of a pair of trabeculæ, and immediately posterior to these there may be a pair of polar cartilages. The side walls in the orbitotemporal region arise from paired orbital cartilages. At the level of the auditory sac a pair of parachordals fuse around the notochord to form the basal plate, and in front of this is added an acrochordal. Behind the basal plate a number of paired pieces form a ring and complete the occipital region. The nasal septum is formed by fusion and upgrowth of the anterior ends of the trabeculæ, and the nasal capsules are formed partly from these and partly from independent cartilages. A pair of auditory capsules formed round the auditory sacs early fuse with the basal plate. The optic capsules, formed round the optic cups, never take any part in the formation of the cranium but

help in the stiffening of the sclerotic. The trabeculæ fuse, but leave a gap between their posterior ends for the hypophysis. Where they meet only at the anterior tips, so that the fenestra is large, the skull is said to be platybasic ; where they fuse down most of their length, it is said to be tropybasic. In this condition, which is found in most teleosts and in amniotes, the trabeculæ grow up to form an interorbital septum which continues the nasal septum backwards, and so confines the brain to the posterior part of the skull. The interorbital septum is less strongly developed in mammals than in birds and reptiles.

In summary, the floor of the chondrocranium is formed from trabeculæ, parachordals and occipital elements ; its side walls from the orbitals, the auditory capsules and the occipitals ; its anterior end from the nasal capsules, while its roof is complete only in the occipital region.

It is logical to try to fit these cartilages into the segmental scheme of the head which we have discussed above, but attempts to do so have not been completely successful. The occipital cartilages more or less clearly come from the sclerotomes of the posterior three or more segments of the head, but the relationship of the other cartilages to their segments is not clear. One scheme is shown in Table VIII. According to this view the trabeculæ and polars represent the pharyngeal elements of the premandibular and mandibular arches respectively, and the parachordals are formed from mesenchyme in segments three and four.

THE BONY SKULL

In all vertebrates above the Chondrichthyes there is at least some replacement of the cartilage by bones formed in it and gradually replacing it (pp. 522–3). In the reptiles, birds and mammals the cartilage bones are much the same, although there is often fusion which obscures their identity in the adult animal. The Anura have much reduced cartilage bones, and the bony fishes have some peculiarities. Taking the cranium topographically and beginning at the front end we find that the nasal septum ossifies as the mesethmoid (Fig. 24.11). This spreads to some extent over the nasal capsules, and in mammals its posterior edge expands to form the cribriform plate, which forms the anterior wall of the brain cavity, and is pierced by many holes for the olfactory nerves. Behind the mesethmoid the side walls

ossify to form the paired orbitosphenoids, which make the orbital septum when this is present, and otherwise make much of the wall of the orbit. The orbitosphenoid may generally be distinguished from other bones near it by the fact that it is pierced by the large optic foramen for the optic nerve. In marsupials, however, this has moved back so that it is confluent with the foramen lacerum anterius, and merely makes a notch in the posterior border of the bone. In many mammals the two orbitosphenoids meet and fuse ventrally and so form part of the floor of the skull. When they do this their ventral portion is called the presphenoid, but it is not strictly a separate bone. The main

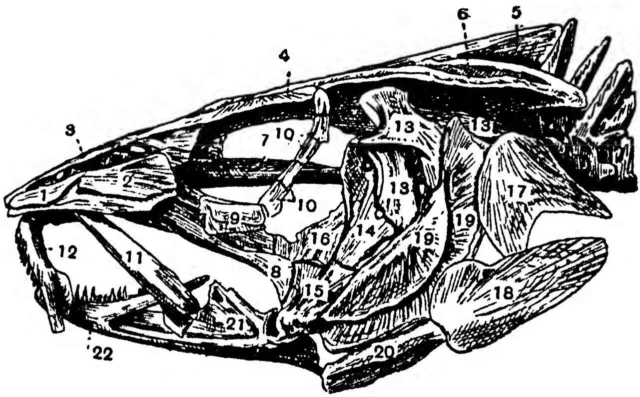


FIG. 27.24.—The skull of a cod, from the left side.—From Reynolds.

1 and 2, Lacrimal; 3, median ethmoid; 4, frontal; 5, supraoccipital; 6, pterotic; 7, orbit; immediately below is the parasphenoid; 8, pterygoid; 9, suborbital; 10, bones of orbital ring; 11, maxilla; 12, premaxilla; 13, hyomandibular; 14, symplectic; 15, quadrate; 16, metapterygoid; 17, opercular; 18, subopercular; 19, preopercular; 20, interopercular; 21, articular; 22, dentary.

part of the floor of the skull, behind the presphenoid when it is present, and in the region of the trabeculæ and basal plate, is formed from a single bone, the basisphenoid. It either retains a hypophyseal fenestra, as in reptiles and birds, or bears on its upper surface a hollow for the pituitary; in mammals it has a somewhat elaborate cave, the sella turcica, excavated in its upper surface. The bone which develops in the side wall above the basisphenoid on each side is generally termed 'alisphenoid', but the bones in the different classes to which this name is applied are quite certainly not all homologous. That of fishes is best called a pterosphenoid, that of reptiles and birds a pleurosphenoid. The 'alisphenoid' of mammals is not an ossification in the chondrocranium, and will be described in its place below.

The auditory capsule forms a large part of the side wall of the skull behind the orbit, and typically ossifies from three centres, to form pro-otic in front, opisthotic behind and below, and epiotic above. Behind these, floor, sides and roof of the skull are all formed by a ring of bones, basioccipital below, supraoccipital above, and an exoccipital on each side.

In mammals the three otic bones fuse to form a single petrosal or periotic, and in some, including man, this fuses with the squamosal and tympanic (see below) to form the temporal ; in marsupials and some others the presphenoid and orbitosphenoids fuse with the mesethmoid to form the sphenethmoid. In addition to these specific fusions there is a general tendency for sutures to become obliterated with age. This tendency is even stronger in birds, where hardly any separate bones are recognisable in the skull of an adult animal. Modern amphibia have the cartilage bones of the cranium much reduced in both number and size. There is a single sphenethmoid (as in marsupials and some extinct tetrapods), and in the ear region there are only the pro-otics. The basisphenoid and the supra- and basioccipitals have also been lost.

In fishes the pterotic and sphenotic in the auditory capsule are bones of mixed origin, i.e. partly cartilage and partly membrane. This is also the condition of the prefrontal, a small bone found above the nasal capsule in many groups.

MEMBRANE BONES OF THE SKULL

As we have seen above, the most primitive known vertebrates had a complete bony covering to the head, and all except the cartilaginous fishes and modern cyclostomes still have some dermal bones which have sunk in from the surface. There is good reason to believe that these were originally dermal denticles or scales, for in some fish they consist not only of bone, which is comparable to the dentine of the placoid scale, but also of an outer layer of either ganoin or cosmine, the materials of which the scales of bony fish are made. Whereas the scales of bony fish (and of tetrapods) have lost their dentine, in the dermal plates on the skull it is the other way about ; the ganoin or cosmine has in general been lost, and the dentine has become bone.

In view of the origin of the dermal bones, it is not surprising

that their homology is difficult, especially in the various groups of fishes. There are, however, no dermal bones in the skulls of

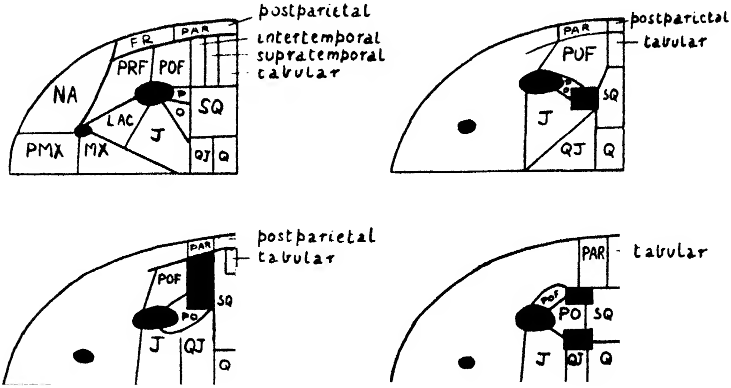


FIG. 27.25.—Diagrams of the main types of reptilian skull. A, anapsid; B synapsid; C, parapsid ; D, diapsid. The facial portion of the skull, shown only in A, is the same in all types ; the nasal foramen, the orbit, and the temporal vacuities, are shown in black.

FR, Frontal ; *J*, jugal ; *LAC*, lacrimal ; *MX*, maxilla ; *NA*, nasal ; *PAR*, parietal ; *PMX*, premaxilla ; *PO*, postorbital(s) ; *POF*, postfrontal ; *PRF*, prefrontal ; *Q*, quadrate ; *QJ*, quadratojugal ; *SQ*, squamosal.

fishes which cannot be traced in tetrapods, except for the gulars and operculars—series of bones which support the operculum.

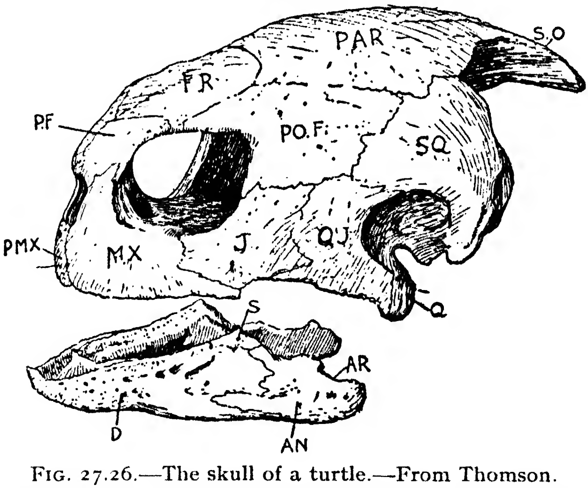


FIG. 27.26.—The skull of a turtle.—From Thomson.

AN, Angular ; *AR*, articular ; *D*, dentary ; *FR*, frontal : *J*, jugal ; *MX*, maxilla : *PF*, prefrontal ; *PAR*, parietal ; *PMX*, premaxilla ; *POF*, postorbital fused with prefrontal ; *Q*, quadrate ; *QJ*, quadratojugal ; *S*, surangular ; *SO*, supraoccipital ; *SQ*, squamosal.

The skull of the cod, which has a fairly complete series of bones, is shown in Fig. 27.24.

The skulls of tetrapods can be reduced to four, or perhaps to three, main types. In the earliest forms, the Stegocephalia and reptilian Cotylosauria, the skull was completely roofed in and covered by membrane bones, the only necessary gaps that were left being the nares, the orbits, and the pineal foramen. The roofing bones fill up the fontanelles, and lie close down on the nasal capsule and on the membrane bones of the upper jaw. Behind, however, they are attached to the auditory capsule only by a paroccipital process from the opisthotic. There is thus a large temporal space between the cartilage bones, which make the side wall of the cranium, and the lateral dermal bones. This space houses the muscles which work the lower jaw. Posteriorly it has an opening, the post-temporal fossa. This type of skull is called anapsid, and is shown diagrammatically in Fig. 27.25 A.

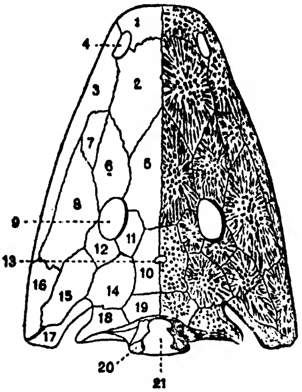


FIG. 27.27.—The skull of *Capitosaurus nasutus*, one of the Stegocephalia. — From Reynolds, after von Zittel.

1, Premaxilla; 2, nasal; 3, maxilla; 4, anterior nares; 5, frontal; 6, prefrontal (*or* lacrimal); 7, lacrimal (*or* adlacrimal); 8, jugal; 9, orbit; 10, parietal; 11, postfrontal; 12, postorbital; 13, interparietal foramen; 14, supratemporal; 15, squamosal; 16, quadratojugal; 17, quadrate; 18, tabular; 19, postparietal; 20, exoccipital; 21, foramen magnum.

The sheet of membrane bones which forms the roof of this skull is a special development of the armour of bony scales which is found on other parts of the body of Stegocephalia. It is not only the roof of the cranium, but stretches over the space between the cranium and the upper jaw (palatopterygoquadrate bar). In most other bony skulls, gaps (the fossæ) appear between the bones of this dermal sheet.

The only living tetrapods with a skull of this type are the turtles and tortoises (Fig. 27.26). It will be seen that a number of bones present in the primitive skull have been lost, and it is possible, though now generally considered improbable, that the completely roofed condition has been secondarily acquired. A stegocephalian skull is shown in Fig. 27.27.

There is some disagreement as to the evolution of the reptilian skull from that of the cotylosaurs, but it is at least certain that two lines have been most successful. In one of these, the synapsid type, the bony arcade covering the jaw muscles has been pierced by a single lower temporal vacuity, which is below the postorbital and postfrontal; it is, in fact, between the dermal bones of the cranium and those of the upper jaw (Fig. 27.25 B). The reptiles which show this condition, the Therapsida, are all extinct, but they left behind them descendants in the mammals. In these, however, considerable

development has taken place. As the brain-box expanded to contain the enlarging brain, the squamosal and parietal spread on the surface of the cranium and became reduced externally, so that the parietal has come to lie completely, and the squamosal largely, inside the jaw muscles. At the same time the postorbital and postfrontal are lost, so that the orbit and the lateral temporal fossa become confluent; the latter, in fact, is no longer recognisable as an opening, for it is simply an empty area above the zygomatic arch, which is all that remains of the plate of bones originally covering the jaw muscles. In monotremes there is an interesting relic of the post-temporal fossa in the form of a narrow canal between the squamosal and the periotic (Fig. 27.28). In artiodactyls and primates the lateral temporal fossa is secondarily separated off from the orbit by downgrowth of the frontal which meets the zygoma. The interparietal present in some mammals, such as the dog, represents fused dermosupraoccipitals.

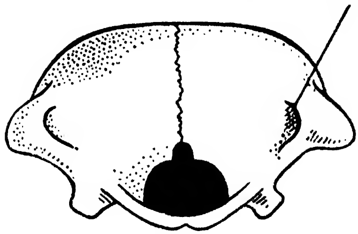


FIG. 27.28.—Skull of *Ornithorhynchus*, posterior view, showing the postsquamosal arcade, probably representing the post-temporal fossa of reptiles.

In the third main reptilian type, the diapsid (Fig. 27.25 D), there are two lateral temporal fossæ, one above and one below the postorbital. The lower is in the same position as that of the synapsids, while the upper pierces the bony arcade of the cranium. The dinosaurs and pterodactyls had skulls of this type, and it is found at the present day in *Sphenodon* and in the Crocodilia (Fig. 27.29). The birds are derived from the diapsid condition by a similar development to that seen in mammals. The frontals, parietals and squamosals have spread over the cranium inside the jaw muscles, and the loss of the postorbital makes the orbit and the two lateral temporal fossæ all confluent.

The fourth and last type, the parapsid or anomapsid, has only a single lateral temporal vacuity, but this time it is above the postorbital and so corresponds to the upper vacuity of diapsids (Fig. 27.25 C). It is now generally agreed that the parapsids do not make a natural group, the single upper temporal vacuity having arisen more than once in widely divergent forms. The Squamata have a skull which is parapsid in form (Fig. 27.30), but they are

almost certainly derived from diapsid ancestors and are now grouped with *Sphenodon* as Lepidosauria. The extinct genus *Prolacerta* shows how the lower vacuity may have been lost ; it had a very small quadratojugal and a thin tapering jugal which

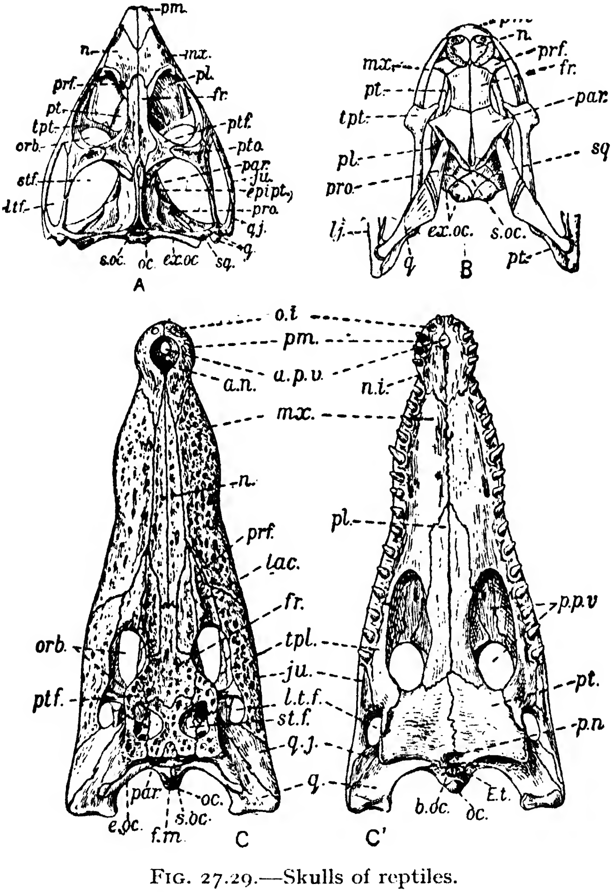


FIG. 27.29.—Skulls of reptiles.

A, Dorsal view of the skull of the tuatara (*Sphenodon*) ; *B*, the same view of the skull of the grass snake (*Natrix natrix*), with small portions of the lower jaw ; *C*, dorsal, and *C'*, ventral views of the skull of a crocodile.

a.n., Anterior nares ; *a.pv.*, anterior palatine vacuity ; *b.oc.*, basioccipital ; *E.t.*, common opening of Eustachian tubes ; *epipt.*, epipterygoid ; *e.oc.*, or *ex.oc.*, exoccipital ; *f.m.*, foramen magnum ; *fr.* frontal *ju.*, jugal ; *lj.*, portion of lower jaw ; *l.t.f.*, lateral temporal fossa ; *lac.*, lacrimal ; *m.x.*, maxilla; *n.*, nasal ; *n.i.*, notch into which fits the fourth tooth of the lower jaw , *o.i.*, opening into which fits the first tooth of the lower jaw ; *o.c.*, occipital condyle ; *orb.*, orbit ; *p.n.*, posterior nares ; *p.p.v.*, posterior palatine vacuity ; *par.*, parietal ; *pl.*, palatine ; *pm.*, premaxilla ; *prf.*, prefrontal ; *pro.* pro-otic; *pt.*, pterygoid ; *ptf.*, post-frontal ; *pto.*, postorbital ; *q.*, quadrate ; *q.j.*, quadratojugal ; *s.oc.* supraoccipital ; *sq.*, squamosal ; *st.f.*, supratemporal foramen ; *tpl.*, or *tpt.*, transpalatine.

For the lizard and turtle, see Figs. 27.30 and 27.26.

Note that the tuatara and crocodiles have both supratemporal and lateral temporal fossæ, the lizard, being without quadratojugal, has no lateral temporal fossa, the snake has neither arcade, and in the turtle there are no fossæ.

nearly reached the quadrate and may have been joined to it by a ligament.

Just as the roof of the skull is covered with dermal bones, so its floor becomes protected by dermal bones originating in the skin of the mouth. There has been much doubt about the homology of these, but it now seems that there are in reptiles an anterior pair, the vomers, underlying the region of the nasal capsules, and posterior to these a single parasphenoid. The vomer of mammals is a small bone formed by fusion of two lateral elements in front of the presphenoid. The parasphenoid is absent from mammals except for vestiges in a few species.

It will be seen by comparing actual skulls with the diagrams in Fig. 27.25 that there is a general tendency to reduction of the dermal bones; intertemporal, supratemporal and tabular, for example, are absent from all modern reptiles. In the Anura the reduction has gone very far, so that only the nasals over the nasal capsule, and the frontals (usually called frontoparietals) are present. In the urodeles the reduction has not gone quite so far, as prefrontal and parietal are present also. By contrast, the dermal bones of the palate, vomers and parasphenoid, are large.

THE VENTRAL SKULL

Below the brain-box and sense capsules lie several skeletal elements which, as we have seen above, have a fairly clear segmental origin. Collectively they may be called the visceral or ventral portion of the skull, but in the tetrapods their posterior portions have no connection with the cranium and are situated outside the head as generally understood, while some of the anterior bones become secondarily and intimately associated with the auditory capsule.

Apart from the rather doubtful derivation of the trabecular and polar cartilages from the segmental elements, the most anterior of these are the supports of the jaws, which are derived from the second or mandibular segment (Table VIII, p. 577). In the embryo there is a single upper-jaw cartilage on each side, called the palatoquadrate, or palatopterygoquadrate, bar, and articulating with each of these to form the lower jaw a single Meckel's cartilage. A similar condition is found in the adult dogfish. Behind this comes a series of skeletal supports, the

hyoid in segment 3 behind the spiracle, and then a branchial or visceral arch behind each gill slit. The primitive division of each of these is probably into four elements on each side, called from above downwards, pharyngo-, epi-, cerato-, and hypo-branchials, and a median ventral basibranchial. Fishes have different variants on this plan ; that of the dogfish has been described on page 316.

In bony fish the upper jaw cartilage ossifies to form at least three bones, the autopalatine, the epipterygoid, and the quadrate ;

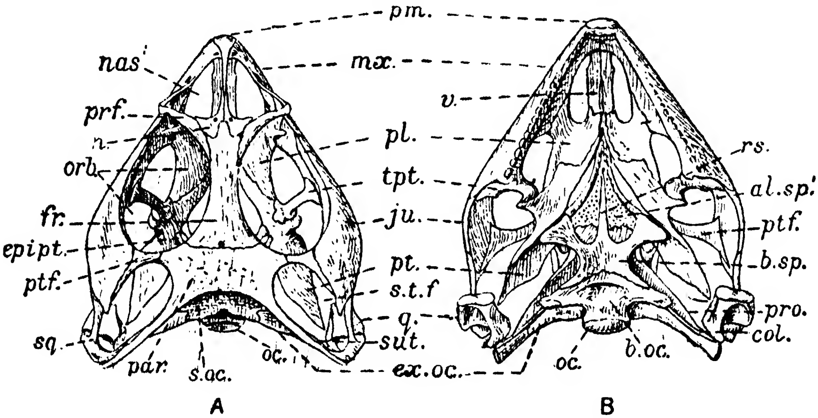


FIG. 27.30.—The skull of the lizard *Uromastix*.

A, Dorsal view ; *B*, ventral view.

al.sp'., Cartilage representing alisphenoid ; *b.oc.*, basioccipital ; *b.sp.*, basisphenoid ; *col.*, columella auris ; *epipt.*, epipterygoid ; *ex.oc.*, exoccipital ; *fr.*, frontal ; *ju.*, jugal ; *mx.*, maxilla ; *n.*, nasal ; *nas'.*, region from which cartilaginous nasal capsule has been removed ; *oc.*, occipital condyle ; *orb.*, orbit ; *par.*, parietal ; *pl.*, palatine ; *pm.*, premaxilla ; *prf.*, prefrontal and lacrimal, fused ; *pro.*, pro-otic ; *pt.*, pterygoid ; *ptf.*, postfrontal and postorbital, fused ; *q.*, quadrate ; *rs.*, rostrum ; *s.oc.*, supraoccipital ; *s.t.f.*, supratemporal foramen ; *sq.*, squamosal ; *sut.*, supratemporal bone (very small) ; *tpt.*, transpalatine ; *v.*, vomer (' prevomer ').

in primitive Crossopterygii there were several pterygoids. In the tetrapods the anterior end of the cartilage does not ossify, and the epipterygoid is the bone which in mammals is called alisphenoid. In most vertebrates except mammals, the quadrate, whether large as in snakes or small and unossified as in the frog, is the part which articulates with the lower jaw ; in the mammals, although present, it has been put to other uses which will be described below.

The upper jaw has various degrees and types of attachment to the dorsal skull, which are classified into three main groups. The simplest, although not necessarily the most primitive, is

known as hyostylic, and is found in most modern Chondrichthyes (Fig. 27.31) and in all bony fish except the Dipnoi. Its characteristic feature is that the chief or only connection between skull and upper jaw is by the hyomandibula (the upper element of the hyoid arch) which is enlarged and bound by ligaments to the otic region and to the quadrate. There may also be a slight connection of jaw to cranium in the ethmoid region. In many primitive Chondrichthyes, and in one modern group, the Notidani, the suspension is called amphistylic; the hyomandibula is used as before, but there are also direct contacts of jaw and cranium in the otic region and farther forward. The extreme tips of the jaws, however, are free from the cranium, and articulate only with each other. It is possible that this is the central primitive type from which the others have been derived.

The last type, autostyly, is found in the Holocephali, the Dipnoi and the tetrapods; the upper jaw is articulated (autodiastyly) or fused (autosystyly) to the cranium, and the hyomandibula takes no part in its suspension. The condition in the Holocephali has probably been achieved independently. In the tetrapods there may be as many as four points where the palatoquadrate bar meets the skull: at the extreme anterior end, in the ethmoid region; by an ascending process from the pterygoid part to the wall of the orbit; by a basal process just behind this, which meets a basipterygoid process from the trabecular or polar cartilage; and posteriorly by an otic process to the auditory capsule. Any of these may be lost or modified. The ethmoid connection fails in amniotes and many urodeles; the ascending process of the pterygoid is absent from birds, but is strongly developed in some reptiles and in mammals, where it grows right into the side wall of the orbit, forming, as has been said, the alisphenoid. The basal connection is prominent in amniotes, but is absent from Anura and Apoda, while the otic process, though always present, is in mammals quite detached from the jaws and takes no part in the suspension (see p. 594). This condition, as well as that of the Squamata and birds, where the quadrate, though in contact with the cranium, is free to move, is called streptostyly, in contradistinction to the monimostyly of crocodiles and chelonians, where the quadrate is firmly fixed to the skull and immovable. A further development of streptostyly, called kinetism, is found in snakes and many birds, especially parrots; there is an articulation across the upper roofing bones, so that

the whole of the face and upper jaw can be raised when the quadrate is swung forward.

Below the palatoquadrate bar and its ossifications dermal bones develop from the skin of the roof of the mouth ; these are

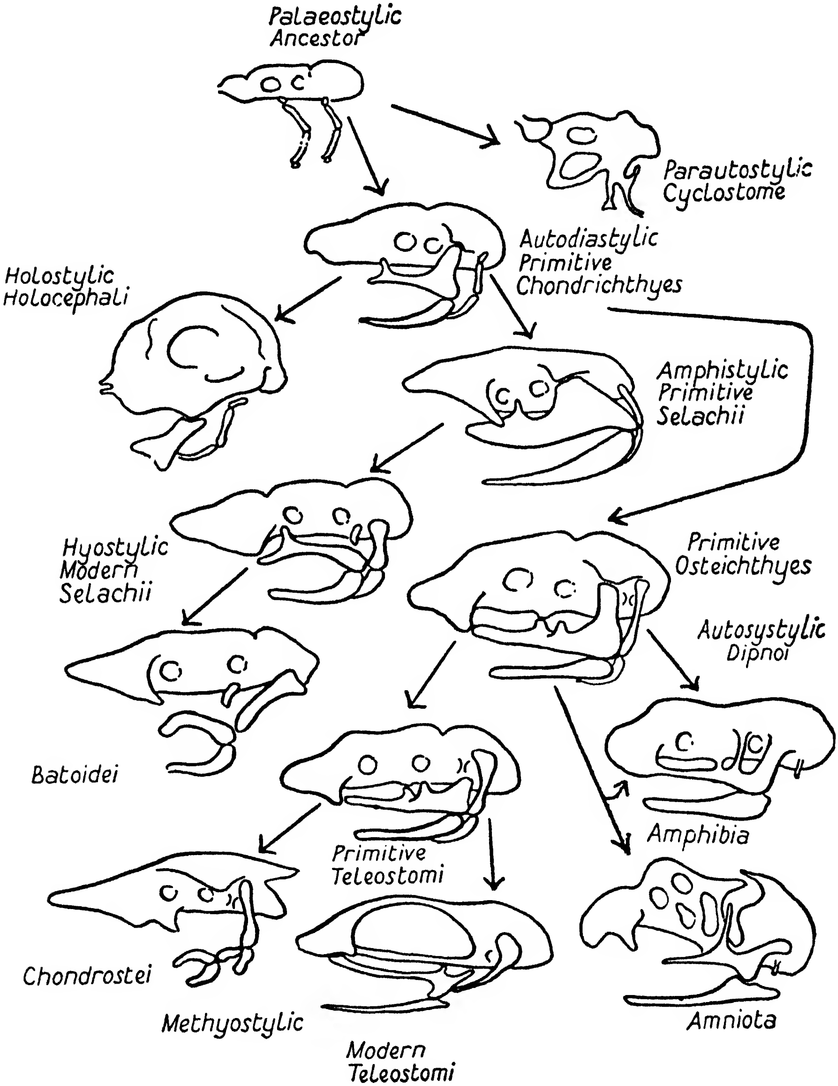


FIG. 27.31.—Diagrams to show the evolution of the jaw suspensions of vertebrates from a hypothetical ancestor in which the visceral skeleton is completely free from the brain case.—From De Beer, *The Development of the Vertebrate Skull*, 1937. Clarendon Press, Oxford.

the paired palatines, dermal pterygoids, and ectopterygoids, with, in front of them, the vomers, which we have already treated as dermal bones of the nasal capsule, to which they are generally closely applied. All four of these may bear teeth. The ectopterygoids are absent from modern tetrapods, but the pterygoids and palatines are usually fairly well developed. The latter tend to be placed horizontally to form the roof of the buccal cavity, while the former tend to lie vertically and bound medially the space containing the jaw muscles. Finally, outside these, another series of dermal bones, the premaxillæ, maxillæ, jugals and quadratojugals, form much of the functional jaw and

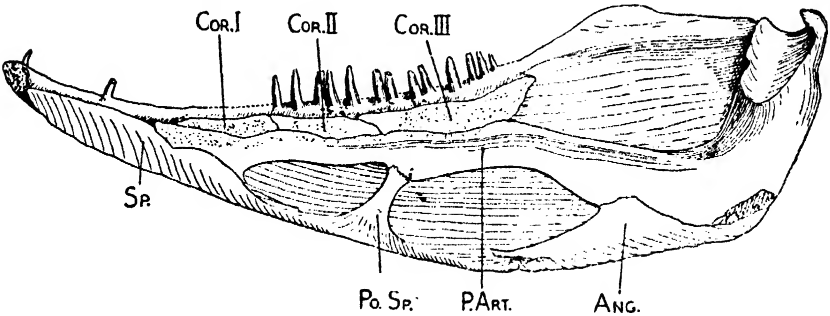


FIG. 27.32.—Lower jaw of *Eogyrinus*. Right half, inner surface.—From Watson, *Phil. Trans. B*, 1926. 224, 189.

ANG., Angular; COR. I, II, and III, coronoid bones; P.ART., prearticular; PO.SP., post-splenial; SP., splenial.

skeleton of the cheek region. It is to be noted that the quadratojugal is not, as might be expected, a combination of quadrate and jugal, but a bone running between those two. It is not present in mammals, where the jugal (also called malar or zygomatic) joins the squamosal. The premaxillæ are usually firmly sutured to each other at the anterior end, but in snakes they are joined only by an elastic ligament, which allows the mouth to stretch in the swallowing of large prey. Premaxilla and maxilla generally bear teeth.

The cartilage of the lower jaw usually ossifies only at the posterior end, to form the articular, which is the part which articulates with the quadrate, but in the Anura there is a small ossification, the mentomeckelian, at the anterior end. Except in the cartilaginous fishes the functional lower jaw consists almost entirely of membrane bones, of which there may be several. They are about at their maximum in Stegocephalia (Fig. 27.32),

where, on the outside, there are a large dentary and smaller coronoid, surangular and angular. All these curve over the edge of the cartilage and are visible on the inside, where there are in addition a prearticular and one or more splenials. Modern tetrapods show various degrees of reduction from this condition, culminating in the mammals which have a single bone, the dentary, which has also taken over from the articular the jointing with the upper jaw; it meets, however, not the quadrate but the squamosal. The so-called 'angulosplenial' of the frog is probably either the prearticular, or that bone fused with the angular.

The relationship of the two pieces which make up the hyoid arch to the elements of the branchial skeleton is not clear, but it is generally assumed that the dorsal element, the hyomandibula, corresponds to an epibranchial element, the ventral ceratohyal to a ceratobranchial, and the median basihyal to the basibranchial. The hyomandibula in fishes generally, as we have seen, suspends the upper jaws. In Amphibia, Reptilia, and Aves it has moved into the middle ear, and become the columella auris which transmits sound waves from the tympanum to the membranous labyrinth. The evidence for this identification depends largely on the relations of the columella to nerves and blood vessels. In mammals the hyomandibula is also in the middle ear, this time as the stapes. The remainder of the hyoid forms, in fishes, an attachment for the muscles which raise and lower the floor of the buccal cavity in breathing, while the branchial arches give strength to the part of the body weakened by the gill slits. In embryonic tetrapods there is a cartilaginous basketwork below the mouth, and in some, such as monotremes and marsupials, some connection with the arches can be made out. Most of the pieces of cartilage coalesce to form the hyoid apparatus which supports the tongue; branchial as well as hyoid elements are included in this, but the exact limits cannot be made out. Its form varies in different groups, but it generally has a flat plate or body, with two or more processes, as we have seen it in the frog, bird, and mammal. There is usually some ossification. The posterior parts persist only as the cartilages of the respiratory system, notably the thyroid, cricoid, and arytenoid cartilages of mammals and perhaps the epiglottal cartilage and tracheal rings.

There remain in the mammalian skull a few bones in the ear

TABLE IX

Bones of the Skull

In the cranium and capsules, plurals indicate paired bones; in the jaws and arches all bones are paired, and plurals imply series of bones.

Region of Skull	Cartilage Bones	Membrane Bones
Cranium	Mesethmoid Orbitosphenoids Presphenoid Basisphenoid Pterosphenoid Pleurosphenoid Basioccipital Exoccipitals Supraoccipitals	Parasphenoid Lacrimals Prefontals Postfrontals Postorbitals Frontals Parietals Intertemporals Supratemporals Dermosupraoccipitals (=Postparietals) (=Interparietal) Tabulars
Nasal Capsules	Mesethmoid in part	Vomers Nasals
Auditory Capsules	Pro-otics, Opisthotics, Epiotics = Periotics	Squamosals
Upper Jaw	Autopalatine Epipterygoid (=Alisphenoid of mammals) Quadrate (=Incus of mammals)	Palatine Dermal pterygoid Ectopterygoid Premaxilla Maxilla Jugal Quadratojugal
Lower Jaw	Articular (=Malleus) Mentomeckelian	Dentary Angular (=Tympanic) Prearticular Surangular Coronoid Splenials
Hyoid Arch	Hyomandibula (=Columella auris) (=Stapes) Ceratohyal (=parts of hyoid of tongue)	
Branchial Arches	Branchial basket	

region for which we have not accounted ; these are the tympanic, which is typically inflated to form a bulla enclosing the middle ear, but which in marsupials and insectivores is a ring, and the first and second of the ossicles (the malleus and incus) ; the third, the stapes, we have already identified as the columella auris. The identification of these bones was made by a comparison of the condition in the embryo with that in the extinct reptiles which are considered to be near the ancestry of mammals (Fig. 27.33). In these therapsids there was a progressive reduction of all the

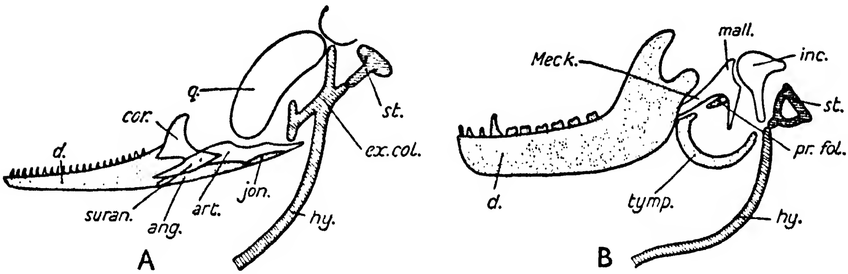


FIG. 27.33.—Diagrams of the arrangement of jaw and auditory ossicles. *A*, in a reptile: *B*, in a mammal. From Young, *The Life of Vertebrates*, 1950. Clarendon Press, Oxford. After Gaupp and Ihle.

ang. Angular ; *art.*, articular ; *cor.*, coronoid ; *d.*, dentary ; *ex.col.*, extra columella ; *hy.*, hyoid ; *inc.*, incus = quadrate ; *jon.*, gonial ; *mall.*, malleus = articular ; *Meck.*, Meckel's cartilage ; *pr. fol.*, prearticular ; *q.*, quadrate ; *st.*, stapes = columella ; *suran.*, surangular ; *tymp.*, tympanic = angular.

bones of the lower jaw except the dentary, until finally all the others became a group of loose bones near the angle of the jaw. Their similarity to the embryonic mammalian condition is obvious, and the detailed homologies may be made as follows. The malleus, which is preceded by cartilage, is the articular ; splints which may be present on the malleus are the surangular (not shown in Fig. 27.33 B) and prearticular ; the incus, since it articulates with the malleus-articular, must be the quadrate ; the stapes bears the same relation to nerves and blood vessels as do the columella and hyomandibula, and so must be identified with those ; and finally the tympanic, from its general shape and topography, must be the angular. This development of the ear ossicles could only have gone on as the old jaw-joint became freed and as the new squamosal-dentary articulation took its place. Some fossil mammals from the Triassic, the docodonts and symmetrodonts, had a lower jaw which is not incompatible with the simultaneous side-by-side existence of the two

joints. It is possible that these two groups gave rise to the monotreme line and to the placental-marsupial line independently, so that the mammals may be an unnatural group.

ALIMENTARY SYSTEM

It was suggested on page 575 that the mouth of vertebrates was formed from an anterior pair of gill slits which coalesced. This accords with the primary function of the other gill slits, and allows for the loss of the more primitive mouth presumably possessed by the invertebrate ancestors. But speculations on such thin grounds are idle, and all that matters is that in all vertebrates there is a mouth which is either terminal or a little way down the ventral surface. The opening leads into a space, also known as the mouth but less ambiguously as the buccal cavity. In most vertebrates this bears teeth of some sort, but they are absent from birds and some smaller groups, such as the turtles. In general, food passes straight through the buccal cavity, and the teeth are mere backwardly directed points which prevent food from escaping, but in most mammals there is a greater or less degree of chewing and the teeth are complex and of different sorts ; the false palate allows breathing to continue while chewing goes on. Some birds also, such as the parrots, chew their food, using the beak for this purpose. A tongue is only developed in the tetrapods, its musculature and skeleton coming from the parts which helped to form the branchial arches. In lower forms, as in the frog and lizards, it is chiefly used for food gathering, but in chewing species it helps in the manipulation of food. It usually bears taste organs, and in the snakes it is an accessory olfactory organ ; in its rapid darting in and out of the mouth it picks up particles of volatile matter, and when it is withdrawn the forked tip fits into two sensory pockets on the roof of the mouth. Mucus-secreting glands open into the buccal cavity of most land-living vertebrates, but it is only in a few mammals and birds, such as man and the fowl, that it contains a starch-digesting enzyme.

The pharynx, the passage from which the gill slits open, is hardly distinguishable in form from the buccal cavity, especially in tetrapods.

The rest of the alimentary canal, or gut, was probably little specialised in the earliest microphagous vertebrates, and that is

still the condition of the lamprey. More often, however, there is some specialisation of parts for different functions, and since the names of these parts are taken from those of mammals we will first list these in order; they are, gullet or œsophagus, stomach, duodenum, ileum, colon, rectum. Duodenum and ileum together make the small intestine, and colon and rectum the large intestine. The gullet is generally a mere passage, down which food passes quickly, and only of much size in long-necked tetrapods. In some birds, particularly seed eaters, its lower part is expanded into a thin-walled storing crop, and in some carnivorous species a limited amount of digestion, bacterial or autolytic, goes on in it. Its wall in pigeons breaks down to form the 'pigeon's milk' on which the young are fed. The first three chambers (rumen, reticulum, psalterium, Fig. 25.17) of the complex 'stomach' of ruminants are formed from the gullet. The anterior end of the stomach is anchored by the œsophagus in the transverse septum, the posterior end by the hepatoenteric ligament which supports the liver, so that as it grows in length it must curve, and it always does so by bulging into the left half of the anterior peritoneal cavity.

The stomach was probably originally a storing organ, and storage is probably still a large part of its function in elasmobranchs, but it usually also carries out preliminary proteolytic digestion, as in mammals. In cyclostomes, lung fishes and many teleosts, where large prey is not taken and storage is not needed, there is no stomach. In many birds there is a division of the stomach into an anterior glandular part, the proventriculus, and a posterior muscular part, the gizzard, so that mechanical and chemical breakdown of the food are largely separated. Gizzard and crop are often found well developed in the same species.

Marking the distinction between stomach and intestine there is usually a sphincter, the pylorus, which regulates the passage of food, another indication of the storage function of the stomach. The division of the small intestine into duodenum and ileum cannot be made out in many lower vertebrates, or indeed in some mammals, and primitively at least its whole length produces enzymes which digest the three main classes of foodstuff, and absorbs the products of the breakdown. Much enzyme production has, however, been transferred to the pancreas, a diffuse glandular outgrowth from its anterior end. To facilitate absorption

the internal surface is increased, especially in herbivores. In the dogfish and other primitive fish there is a spiral valve, which in effect divides up the lumen of the intestine into a long helical tube, and this was probably the primitive condition. In teleosts and tetrapods the same result is achieved by an external coiling of the intestine, with increase of its length, which reaches a maximum in herbivorous mammals, where it may be twenty times the length of the body. The surface is also increased in mammals, and to a lesser extent in other groups, by internal finger-like projections or villi.

The colon is important chiefly in land forms, where it absorbs water. In fishes it is usually only a short passage for storing fæces, a function carried out in mammals by the rectum. This last is homologous with the part of the gut which in most vertebrates, except the teleosts, receives the genital and urinary ducts, and is called the cloaca. This also is a storage place, from which fæces are voided at intervals.

Blind diverticula of the gut, or cæca, occur at various positions in most vertebrates, but their distribution is often irregular even within a class. Their function is usually that of allowing increased bacterial digestion or absorption of water, and their commonest position is at the junction of small intestine and colon.

In the chick and some other animals the liver arises from two outpushings of the mid-gut about midway between the anterior intestinal portal and the transverse septum (pp. 662 and 655); one becomes the liver itself, the other the gall-bladder, the bile-duct coming from either or both. The liver expands in the ventral mesentery, which persists above it as the hepatoenteric ligament, in which run the bile-duct, hepatic artery and hepatic portal vein, and below, anchoring the liver to the ventral body wall, as the falciform ligament. Whatever its origin, the liver is very much more than a gland, its cells in all vertebrates carrying out many complex chemical reactions (pp. 535–6).

The pancreas arises from several outpushings just behind the bile-duct.

RESPIRATORY SYSTEM

We have already covered incidentally most of the more important points in this. The primitive place for gas exchange in animals is undoubtedly the skin, and in all species where this

remains moist and unprotected by a thick epidermis it is inevitable that diffusion along a concentration gradient will take place. About a third of the oxygen uptake, and three-quarters of the carbon dioxide loss, goes on through the skin in a resting edible frog, and some salamanders have neither gills nor lungs, and so presumably breathe entirely through the skin. In most vertebrates, however, the skin is too thick to be more than an accessory respiratory organ, and in the primarily aquatic forms, gills, developed on the walls of the gill slits which are characteristic of chordates, are the chief site of gas exchange. We have already seen that *Branchiostoma* has a large number of these, and that in the fishes there is on the whole a reduction to about five pairs, with an anterior smaller pair, the spiracles. Like the gills of lamellibranchs (p. 274) these gill slits were probably originally nutritive, not respiratory, in function. All the early vertebrates, as well as the protochordates, appear to have been microphagous, and to have got their food by maintaining a current of plankton-containing water over a mucous surface. For this purpose some division of the stream of water into small channels is clearly useful, so that the advantage of the gill slits is obvious. They could, incidentally, if their walls were thin enough, absorb oxygen, and it might be an advantage for them to increase their surfaces to do so. With the abandonment of microphagy their respiratory function would be left, and would increase in importance with increasing size of the animal.

The gill slits are formed by pockets which grow out from the pharynx and meet corresponding depressions growing in from the skin ; they are thus lined partly by endoderm and partly by ectoderm (p. 654). In fish the gills are developed from the outer ectodermal part, so that they are, as most gills are, expansions of the skin. The posterior surface of the last slit generally has no gill, and in many teleosts the anterior surface of the first slit is often bare, but otherwise each slit generally has a gill on each surface ; such a gill is called a hemibranch, to show that it is half the complete complement of a slit. In sharks the gills are merely crinkled expansions of the wall of the slit, and so are called lamellar, but in teleosts they are produced into long streamers projecting into the outer world—the filamentar type (Fig. 27.34). The slits are here close together, and their external openings, and the gills, are covered with a backwardly projecting operculum, supported by special bones (p. 583).

The front surface of the spiracle usually has a small gill, called a pseudobranch, which is probably functionless. In the tetrapods the spiracle persists as the Eustachian tube (p. 467) but the other slits have no more than a temporary existence—relatively lengthy and functional in the larvæ of Amphibia, transitory in the amniotes.

Where the oxygen concentration is low, it seems that the

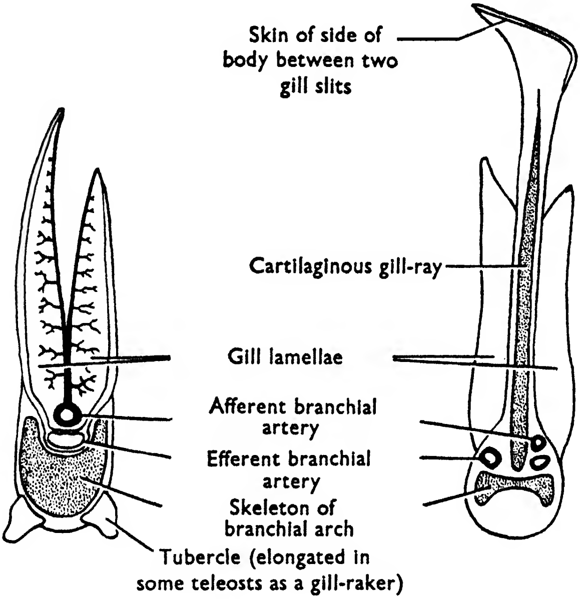


FIG. 27.34.—Transverse sections through the gill arches of a dogfish (on the right) and a cod.—Redrawn from Sedgewick, after R. Hertwig.

internal gills of the gill slits are inadequate to obtain all that the animal needs, and various fishes living under such circumstances have developed two types of accessory respiratory organ. The first is the external gill, a vascular outgrowth of some other part of the body, analogous to similar structures in many other phyla. In modern fishes they are found only in the larvæ of *Polypterus*, *Lepidosiren* and *Protopterus* (p. 552) but they are found in all larval Amphibia and so were presumably present in the ancient crossopterygians from which these were derived. In the perennibranchiate urodeles, which do not metamorphose, they

persist throughout life, and are the only respiratory organs, apart from the skin, in the adult.

The other accessory respiratory organ, the lung, was much more revolutionary, since its value depended on the changed habit of coming to the surface to breathe air, and it led to the evolution of the tetrapods. It arises in ontogeny as an outgrowth of the pharynx, but pushes the surrounding splanchnopleure in front of it so that it is covered with mesodermal connective tissue.

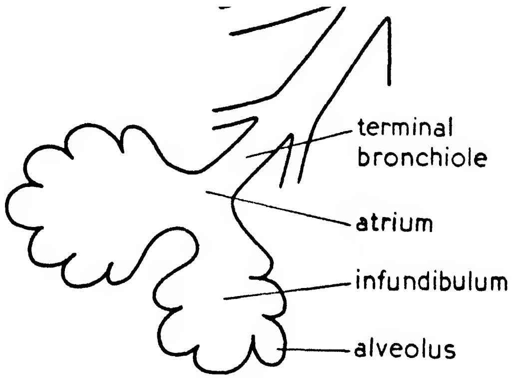


FIG. 27.35.—Diagram of a small part of a mammalian lung, showing the ending of a bronchiole.

The lungs were almost certainly in their origin ventral; such a condition is found in the actinopterygian *Polypterus*, but in other fish either the lung by itself has moved dorsally, or its opening has changed its position also. A functional lung is found amongst fishes in the Dipnoi, and in *Polypterus*, *Amia*, and *Lepidosteus* of the actinopterygians. In adult Amphibia it is the usual and in amniotes the only respiratory organ, and its functional evolution may be traced in the types that we have studied. In the frog it is a simple sac, with only slight ridges on the internal surface; in lizards there are various degrees of increase and subdivision of these ridges, giving a much increased area for gas exchange; and in the mammals the subdivision has gone to its maximum with a branching system of bronchioles leading to small alveoli packed together to form a spongy mass (Fig. 27.35). In birds a

similar end has been obtained by more efficient means, as with the development of air sacs 'dead space' has been eliminated (pp. 406–7).

Most Actinopterygii have no lungs but instead there is a single

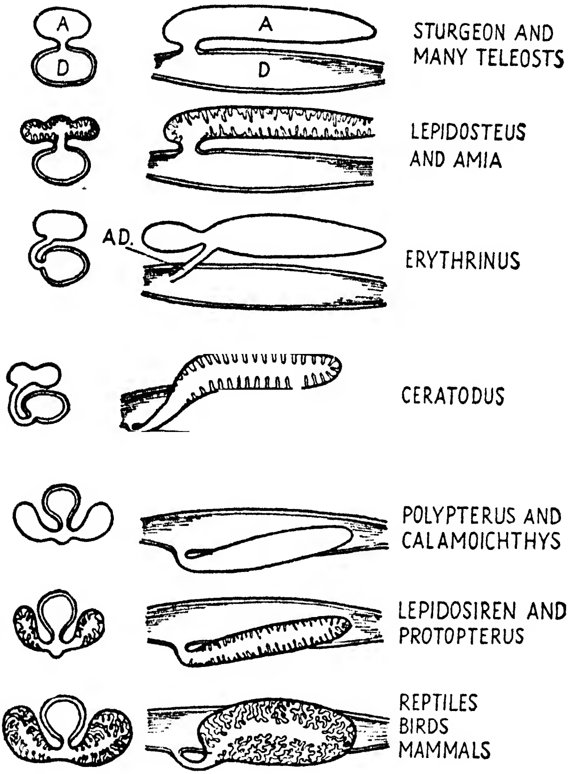


FIG. 27.36.—The air-bladder of various fishes, seen from in front and from the left side.—From Young, *The Life of Vertebrates*, 1950. Clarendon Press, Oxford. After Dean and Wilder.

dorsal swim-bladder which may be open to the œsophagus or other part of the gut (physostomatous) or closed (physoclystous). In both types there is usually a special vascular portion of the wall which can secrete and absorb gas. The fish can therefore raise or lower its specific gravity and so adjust itself to the depth at which it is swimming. In the order Ostariophysi, which includes the carp, the swim-bladder functions as a sound resonator, and a

chain of small bones derived from the vertebræ, the Weberian ossicles, runs from the bladder to the inner ear. In some physostomatous forms, with an opening to the pharynx, air is occasionally taken in through the mouth.

The occurrence of a lung in all the more primitive bony fishes has led to the general opinion that this is the more primitive structure, from which the swim-bladder was derived. The origin of the Actinopterygii was probably in fresh water, but their great expansion was in the sea; here there was no shortage of oxygen, and the lung, developed for respiration in marshes or sluggish rivers, could be put to hydrostatic uses. It is doubtful if any teleost uses its air-bladder as a lung, although some of the primitive physostomatous forms may do so. Many teleosts have taken to breathing air, but they do so either, like the eel, through the general body surface, or through specially developed structures such as the air chamber above the head in the climbing perch (*Anabas*) of India. In many flat-fishes, which neither breathe air nor change their level in the sea, there is no air-bladder at all.

CIRCULATORY SYSTEM

All vertebrates are large enough and active enough to need a circulatory system, and in all of them it is based on the same plan: a ventral part in which the blood flows forwards, and a dorsal in which it flows backwards, the two being connected by capillaries. At some point there are interpolated respiratory organs—lungs, gills or skin—and in the ventral portion is a pumping organ, the heart. This makes a new division in the system, so that vessels which take blood from the heart to capillaries are called arteries, and those which return it are called veins.

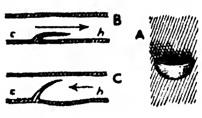


FIG. 27.37.—Diagrams of a valve in a vein.

A, Part of the wall of the vein from within; *B*, longitudinal section of the vein, showing the position of the valve when blood flows from the direction of the capillaries (*c*) towards the heart (*h*); *C*, similar section showing how reflux is prevented by the valve.

The original plan of the vertebrate circulatory system seems to have been for the main vessels to be paired, but there is a general tendency for their fusion to form single median tubes. The blood vessels are formed as tubes of mesoderm surrounding spaces where the cells have broken down to form blood; their

main outlines are shown in Fig. 28.25. The first ventral vessels to appear in ontogeny are a pair of vitelline veins which lead from the splanchnopleure of the yolk sac and fuse in the anterior intestinal portal (p. 662) to form a single subintestinal vessel. In the region just anterior to the transverse septum, which divides the cœlom into anterior and posterior cavities, either just before or just after fusion, swelling and specialisation begin and the heart is formed. In some groups the walls of the heart are formed prematurely by foldings of splanchnopleure and somatopleure, and it begins to beat before any blood reaches it. Primitively the heart has four chambers, which are, from behind forwards, a thin-walled sinus venosus, a slightly thicker-walled auricle (or atrium), a strongly muscular ventricle, and a thick-walled and many-valved conus arteriosus. The dogfish shows this condition except that the heart has been bent into an S-shape, so that the sinus venosus comes to lie above, and the auricle above and slightly in front of, the ventricle (Fig. 21.11). All fishes are somewhat similar.

Anterior to the heart paired ventral aortæ continue, and from them blood is forced dorsally between the gill pouches in branchial arches. From these it runs forwards into the head mesoderm, and backwards in either one or two dorsal aortæ above the dorsal mesentery of the gut and below the notochord. At the posterior end (the blastopore in primitive forms) a vitelline artery runs on each side of the gut into the yolk that lies below it. These become joined to the vitelline veins by sinuses and a complete circulation is established.

Meanwhile another vessel, the cardinal sinus, has appeared on each side of the notochord ; the two pass down the transverse septum, which marks their division into anterior and posterior portions, and blood from them drains into the sinus venosus. Dorsal aorta and cardinal sinuses are at first connected by many fine vessels, but these become restricted to pairs between the somites, the vertebral arteries and veins ; this is well seen in the tail of teleosts.

With the development of lungs, oxygenated blood is returned to the heart by pulmonary veins before it is sent round the body, so that two streams of blood, one oxygenated and one not, enter the heart. The pulmonary veins of *Polypterus* lead into the sinus venosus, but those of the Dipnoi go straight to the left side of the auricle, which is partially divided by a septum into right

and left halves. This condition, which presumably also occurred in the ancestors of the tetrapods, made possible the next stage, which we find in most Amphibia, where there are two separate auricles in parallel. The right receives deoxygenated blood from the sinus venosus (though where, as in the frog, the skin or buccal cavity is an important respiratory organ, the blood in the sinus venosus is ' mixed '), while the left receives oxygenated blood from the two pulmonary veins. In both Dipnoi and Amphibia there is only a single ventricle (though in the former there is a slight septum), and it has generally been assumed that mixing of the two streams of blood is prevented by the shape of the cavity and the valves in the conus. It is now known, however, that in the frog there is almost complete mixing. In the reptiles the arrangement of the auricles is similar to that in the frog except that the sinus venosus has disappeared, but there is an almost complete range of subdivision of the ventricle into right and left halves and the conus is lost. In *Lacerta viridis* the ventricular septum is incomplete, but there is considerable separation of the arterial and venous streams, and little difference between the types of blood conveyed by the two systemic arches. In crocodiles, where the connection between the two ventricles is only by a small hole, the foramen of Panizza, there can be hardly any mixing at all. As we shall see later, however, there is no separation in the systemic system, so that the body receives both oxygenated and deoxygenated blood from the heart. In mammals and birds there are two separate ventricles, and the aorta arises from one only of them, while the other feeds the pulmonary arteries. The body thus receives only oxygenated blood. This result is arrived at by different means in the two groups. In both the conus is lost. Since there is a partial interventricular septum in *Lepidosiren*, and since all modern amphibians are specialised by reduction in many parts of the body such as the skeleton, it is possible that they have lost also an interventricular septum that their ancestors possessed.

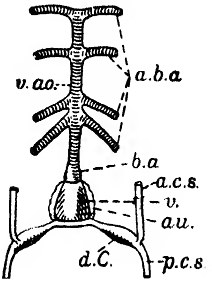


FIG. 27.38.—A semi-diagrammatic ventral view of the heart and neighbouring blood vessels of a cod.

a.b.a., Afferent branchial arteries; *a.c.s.*, anterior cardinal sinus; *au.*, auricle; *b.a.*, bulbus arteriosus; *d.C.*, ductus Cuvieri; *p.c.s.*, posterior cardinal sinus; *v.*, ventricle; *v.ao.*, ventral aorta.

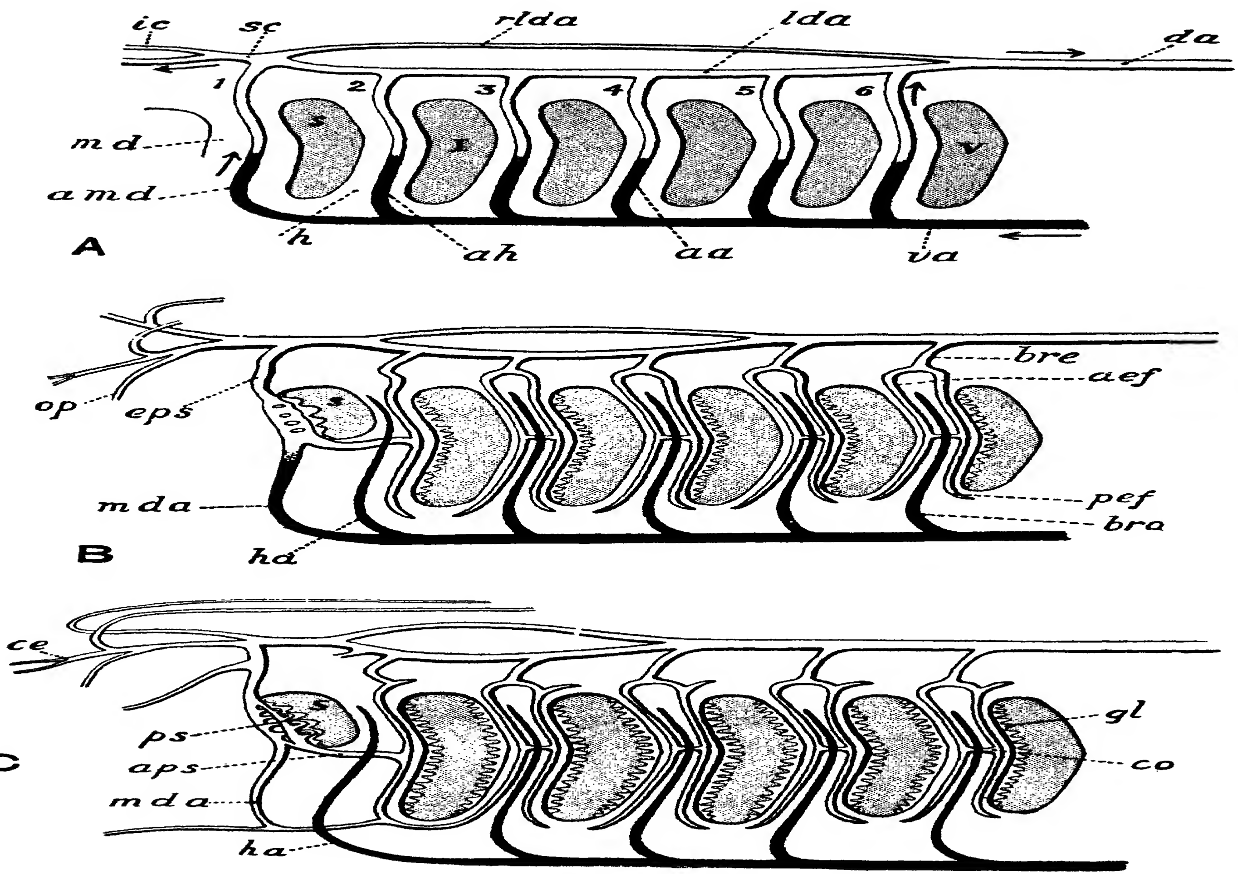
The conus arteriosus leads forwards into the ventral aorta,

which sooner or later divides into right and left halves, which represent the anterior portions of the original paired vitelline vessels. From the lateral ventral aortæ, afferent branchial arteries lead to the gills, which are drained by efferent branchial arteries which join to form lateral dorsal aortæ. A small part of the blood in these flows forwards to the head, but most goes backwards. The two aortæ join at some point not much farther back than the heart and form a single vessel. From this arise the main arteries which supply the body, paired to limbs, kidneys and gonads, unpaired to the gut.

BRANCHIAL ARTERIES

Even in those vertebrates in which the gills persist throughout life as the only respiratory organs, complications arise in the branchial vessels, and as lungs progressively replace gills further changes occur. Before we discuss these, some points of nomenclature must be made clear. In tetrapods the lateral ventral aortæ, after supplying the gills or giving off whatever branches are derived from the branchial vessels, continue forward as the external carotids, which supply some of the outer parts of the head. In fishes these vessels, which contain only deoxygenated blood, are vestigial, and the name external carotid should not be used for the quite different vessels which functionally correspond to them, but are branches of the anterior prolongations of the lateral dorsal aortæ. These last vessels in all vertebrates supply the brain, and are called internal carotids. Each also bears a branch, the orbital of fishes or stapedial of amniotes, which passes near or through the hyomandibula (=stapes), and together with ophthalmic and optic branches of the internal carotid supplies some of the outer parts of the head. The division of the supply of these between the external carotid and the dorsal arteries differs between the classes and even within a class. The vessel in lizard and frog which is usually called the lingual is the external carotid (Fig. 22.29). In fishes the lateral dorsal aortæ fuse not only posteriorly but for a short distance anteriorly as well. The result is a closed loop, of varying size, called the cephalic circle. It is from the anterior part of this, or from a short median aorta that runs forwards out of it, that the internal carotids arise (Fig. 27.40).

If it be assumed, as has been suggested on pages 573–4, that the head was originally segmented nearly to its anterior end,


ic
sc
rlda
lda
da
1
2
3
4
5
6
md
amd
h
ah
aa
va
A
op
eps
bre
aef
pef
bra
mda
ha
B
ce
ps
aps
mda
ha
gl
co
C

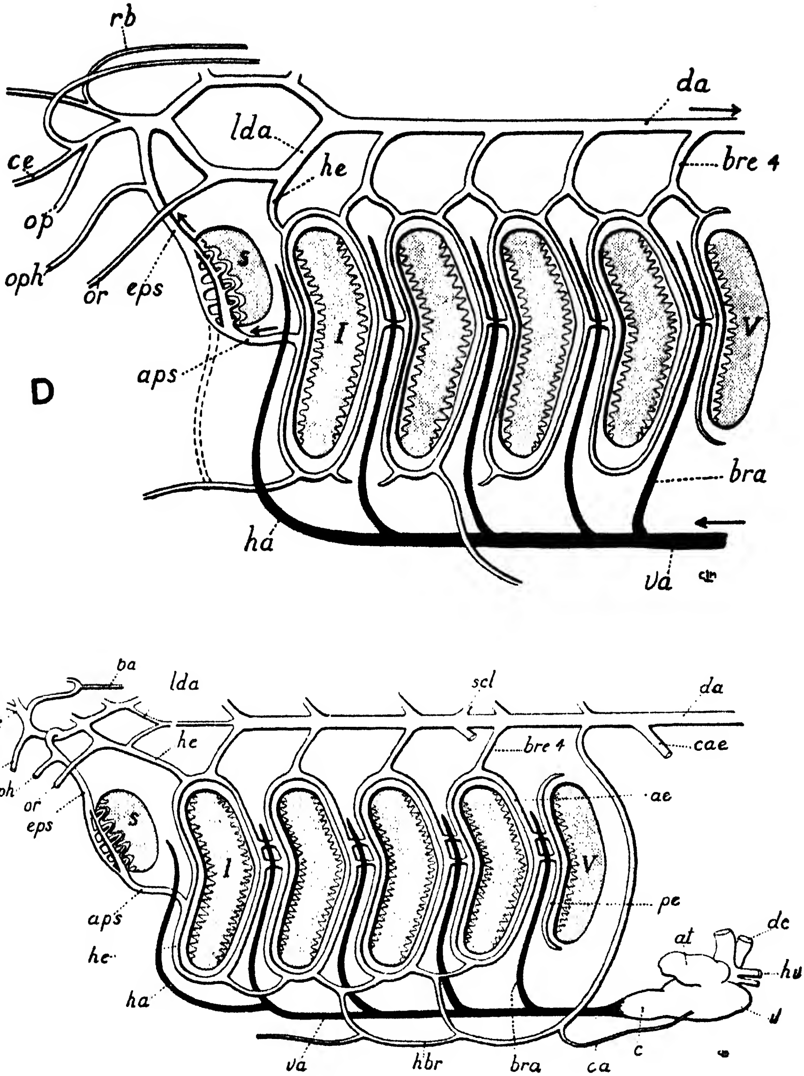


FIG. 27.39.—Diagrams to show the development of the embryonic arterial arches in a selachian..—From Goodrich, *Studies on the Structure and Development of Vertebrates*, 1930. Macmillan, London.

aa, and ***bra***, Afferent branchial ; ***ae***, and ***aef***, anterior efferent ; ***ah***, and ***ha***, afferent of hyoid bar ; ***amd*** and ***mda***, afferent of mandibular bar ; ***aps***, afferent pseudobranchial anastomosis ; ***at***, auricle ; ***bre***, and ***bre*** 4, epibranchial ; ***ba***, basal artery ; ***c***, conus ; ***ca***, cardiac ; ***cae***, cœliac ; ***ce***, cerebral ; ***co***, cross commissural ; ***da***, median dorsal aorta ; ***dc***, ductus Cuvieri ; ***eps***, efferent pseudobranchial ; ***gl***, gill lamellæ ; ***h***, hyoid bar ; ***hbr***, hypobranchial ; ***he***, efferent of hyoid bar ; ***hv***, hepatic veins ; ***ic***, internal carotid ; ***lda***, left lateral dorsal aorta ; ***md***, mandibular bar ; ***op***, optic ; ***oph***, ophthalmic ; ***or***, orbital ; ***pe*** and ***pef***, posterior efferent ; ***ps***, mandibular pseudobranch ; ***rb***, posterior cerebral ; ***rlda***, right lateral dorsal aorta ; ***sc***, sinus cephalicus ; ***scl***, subclavian ; ***v***, ventricle ; ***va***, ventral aorta ; 1–6, primitive arches ; I–V, branchial gill slits ; *S*, spiracle.

one would expect the arteries to correspond, and one may regard the branches of the orbital or external carotid as the relics of those of the mandibular and premandibular segments. From the spiracle back the segmental arrangement is clearer although it is modified by the fact that the gills are intersegmental, and in tetrapods by their loss. The simple scheme is that shown in Fig. 27.39 A which shows an embryo shark; in the adult, the greater part of the dorsal portion of the branchial vessels disappears, and is replaced by new efferent branchial arteries which are so arranged that blood from the afferent or ventral portion of the vessels has to pass through the capillaries of the gills before reaching them. Stages in their development, and in that of their cross-connections, are shown in Figs. 27.39 B–E. At the same time the most dorsal parts of the original vessel shift to come opposite the gill slits instead of the gill bars; they are the vessels commonly dissected under the name of efferent branchial arteries, but also called epibranchials. In teleosts a very similar arrangement is reached by loss of the original ventral portion of the branchial vessels, and their replacement by new secondary afferent vessels. In fishes with a lung, it is supplied by a vessel from the last epibranchial.

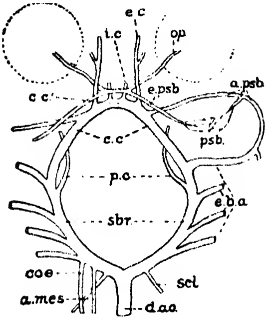


FIG. 27.40.—A diagrammatic ventral view of the dorsal arterial system of a cod.

a.mes., Anterior mesenteric artery; *a.psb.*, afferent pseudobranchials; *c.c.*, carotids; *c.c'.*, anastomosis between the internal carotids which completes the *circulus cephalicus*; *coe.*, cœliac; *d.ao.*, dorsal aorta; *e.b.a.*, efferent branchial; *e.c.*, orbitonasal or 'external carotid'; *e.psb.*, efferent pseudobranchial; *i.c.*, internal carotid; *op.*, ophthalmic; *p.c.*, orbital or 'posterior carotid'; *psb.*, pseudobranch; *sbr.*, suprabranchial; *scl.*, subclavian artery.

In the embryos of Amphibia the branchial circulation is essentially fish-like (Fig. 27.41), but in the adults, and even more in reptiles, there are considerable modifications. The chief of these are: a splitting of the ventral aorta into right and left halves, loss of the dorsal aorta between the third and fourth arches, loss of the fifth arch, loss of the dorsal part of the sixth epibranchial so that the pulmonary has no connection with the dorsal aorta; and separation of the pulmonary from the ventral aorta right back to the conus. These are not all present in all groups. A summary of the derivations of the main vessels, and of some of the chief names used, is as follows:

Internal carotid : anterior prolongation of dorsal aorta, plus third arch.

External carotid : anterior prolongation of ventral aorta.

Common carotid : ventral aorta between third and fourth arches.

Carotid gland or labyrinth : remains of capillaries of second gill.

Carotid duct [1] : dorsal aorta between third and fourth arches. It persists in the adults of Apoda, some Urodela (e.g. *Triton*), and some Reptilia (e.g. *Sphenodon, Lacerta*).

Systemic arch : basal portion of ventral aorta, plus fourth arch, plus lateral dorsal aorta.

Fifth arch : persists in adult Urodela.

Ductus arteriosus [1] : dorsal portion of sixth epibranchial. It persists in Apoda, Urodela, and many Reptilia (e.g. *Sphenodon, Alligator*, some Chelonia). In Anura and in other amniotes, including mammals, it is represented by a fibrous strand.

Pulmonary : a split-off part of the ventral aorta, plus the ventral portion of the sixth arch.

Further development has taken place along two main lines. In the therapsidan type, which has given rise to the mammals, the ventral aorta becomes spirally split to its base, so that the pulmonary trunk comes from the right side of the heart, the aortic trunk (which forms systemics and carotids) from the left. At the same time the ventricle becomes divided into right and left halves, so that the pulmonary contains only deoxygenated blood and the aorta only oxygenated. The posterior portion of the right lateral dorsal aorta distal to the subclavian (i.e. the right systemic) atrophies, so that what is called the right subclavian includes also a portion of the dorsal aorta. Neither this condition nor anything approaching it is found in living reptiles, but presumably the extinct Therapsida, from which the mammals are derived on grounds of skull structure, had something intermediate between that of the mammals and that of the Amphibia. The relationship of these two is shown in Fig. 27.42.

In the culmination of the sauropsidan type in the birds a similar result has been reached by different means. Not only has the pulmonary been separated from the aorta to come from

[1] Both carotid duct and ductus arteriosus have in the past been called ductus Botalli.

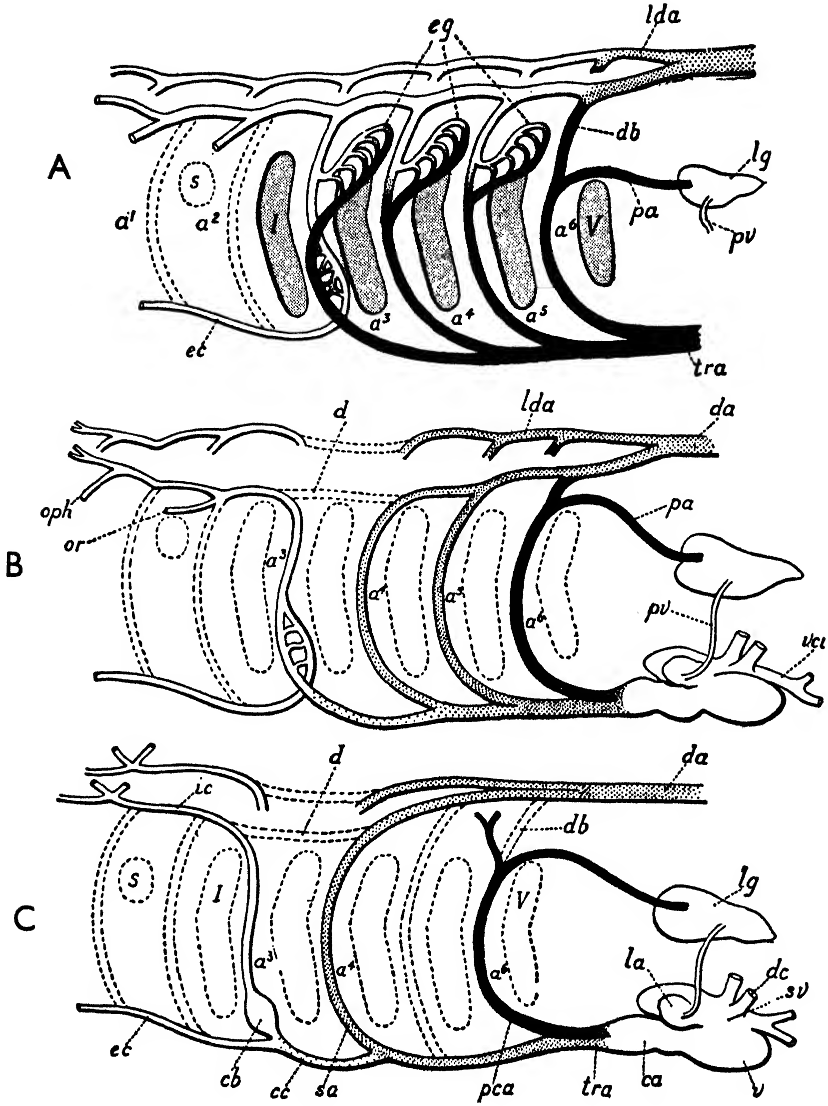


FIG. 27.41.—Diagrams to show the development of the arterial arches in Amphibia.—From Goodrich, *Studies on the Structure and Development of Vertebrates*, 1930. Macmillan, London.

A, Larval urodele ; *B*, adult urodele ; *C*, adult anuran. Left side view. Vessels carrying mostly arterial blood, white ; venous blood, black ; mixed blood, stippled.

a^{1-6}, Primary arterial arches ; *ca*, conus arteriosus ; *cb*, carotid body ; *cc*, common carotid ; *d*, carotid duct ; *da*, median dorsal aorta ; *db*, ductus Botalli ; *dc*, left ductus Cuvieri ; *ec*, external carotid ; *eg*, blood vessels of external gill ; *ic*, internal carotid ; *la*, left auricle ; *lda*, lateral dorsal aorta ; *lg*, lung ; *oph*, ophthalmic ; *or*, orbital ; *pa*, pulmonary artery ; *pca*, pulmocutaneous arch ; *pv*, pulmonary vein ; *s*, closed spiracle ; *sa*, systemic ; *sv*, sinus venosus ; *tra*, truncus arteriosus ; *v*, ventricle ; *vci*, inferior caval vein.

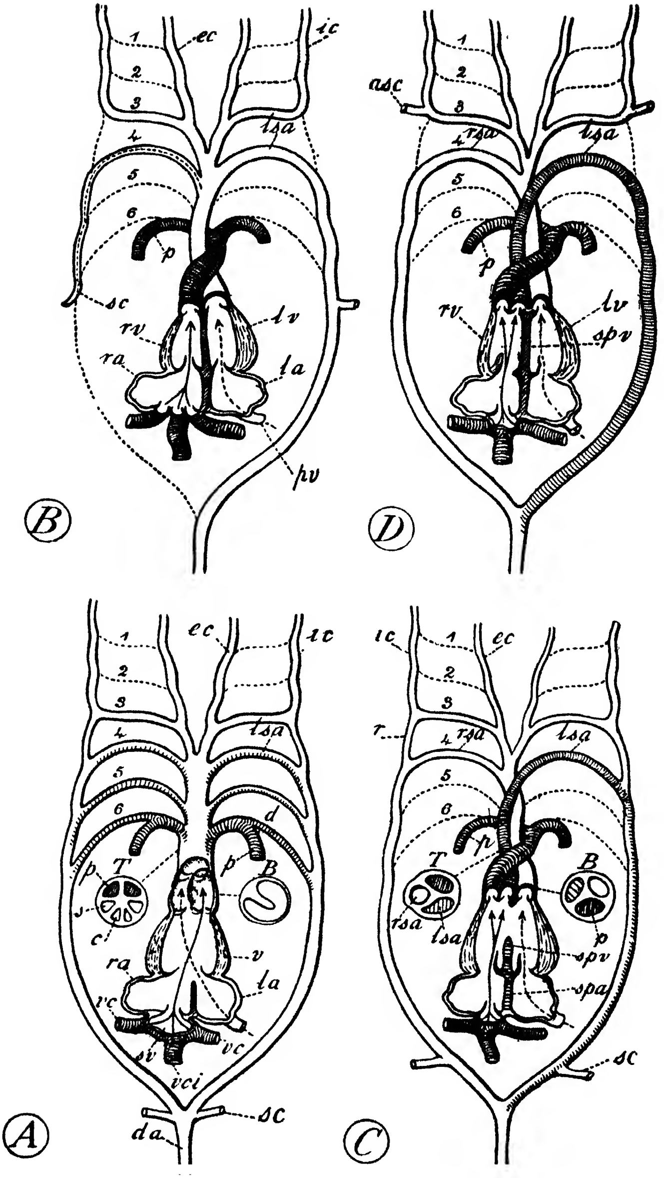


FIG. 27.42.—Diagrams of heart and aortic arches. Ventral view with heart untwisted, to bring the chambers into one plane and the ventricle anterior.—From Goodrich.

A, Amphibian ; *B*, mammal ; *C*, most reptiles ; *D*, crocodile. In *A* and *C*, B and T are sections of the proximal and distal parts of the truncus arteriosus respectively.

asc, Anterior subclavian ; *c*, carotid arch ; *d*, ductus Botalli ; *da*, dorsal aorta ; *ec*, external carotid ; *ic*, internal carotid ; *la*, left auricle ; *lsa*, left systemic arch ; *lv*, left ventricle ; *p*, pulmonary artery ; *pv*., pulmonary vein ; *r*, ductus arteriosus ; *ra*, right auricle ; *rsa*, right systemic arch ; *rv*, right ventricle ; *s*, systemic arch ; *sc*, subclavian ; *spa*, interauricular septum ; *spv*, interventricular septum ; *sv*, sinus venosus ; *v*, ventricle ; *vc*, superior caval vein ; *vci*, inferior caval vein ; 1–6, original embryonic arterial arches.

the right side of the heart, but the aorta itself is split so that one part comes from each side of the ventricle, and, by an apparently pointless cross-over, that which comes from the right forms the left systemic, and vice versa. Except for the connection through the ductus Botalli, both carotids come entirely from the right dorsal aorta (=systemic) and so connect only with the left side of

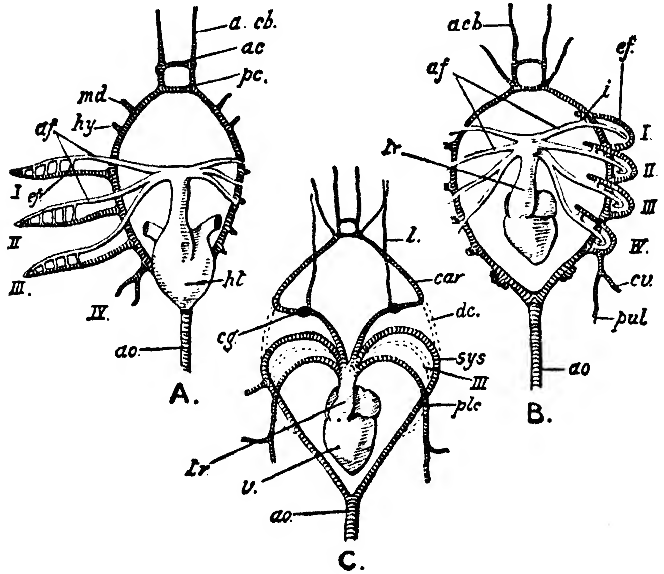


FIG. 27.43.—Diagrams of the heart and chief arteries of a tadpole.—From Bourne.

A, The vessels of a tadpole at the stage when three external gills are present; *B*, the arrangement when secondary gills are in use; *C*, the adult arrangement.

a.c., Anterior commissural vessel; *a.cb.*, anterior cerebral artery; *af.*, afferent branchial arteries; *ao.*, dorsal aorta; *car.*, carotid artery; *c.g.*, carotid gland; *cu.*, cutaneous artery; *d.c.*, ductus caroticus; *ef.*, efferent branchial arteries; *ht.*, heart; *hy.*, efferent hyoidean artery; *i.*, connecting vessel; *l.*, lingual artery; *md.*, efferent mandibular artery; *p.c.*, posterior commissural vessel; *pl.c.*, pulmocutaneous arch; *pul.*, pulmonary artery; *sys.*, systemic arch; *tr.*, truncus arteriosus; *v.*, ventricle; *I.–IV.*, branchial aortic arches.

the heart (Fig. 27.42 C). In the crocodile, with its almost completely divided ventricle, this means that while the carotids contain oxygenated blood, the median dorsal aorta, formed by the junction of the two systemics, contains mixed blood. In most reptiles the left systemic is much smaller than the right. In birds the ventricle is completely divided, and the left systemic is suppressed, so that an exact functional similarity to mammals is achieved (Fig. 23.19). While the sauropsid type of circulation is characteristic of diapsid reptiles, the differences in the details

of the arches in the Chelonia, Crocodilia and Lepidosauria are so great as to suggest an early splitting of the diapsid line.

VEINS

The blood is returned to the heart by four main systems of veins, those which drain the gut (hepatics and hepatic portals), the dorsal body-wall and main muscles (cardinals or venæ cavæ), the ventral body-wall (abdominals) and the lungs (pulmonaries). All of these are originally paired, but there is a general tendency, both in ontogeny and in phylogeny, for them to join to form, or be replaced by, single vessels.

As we have seen, the two vitelline veins fuse to form a subintestinal vessel. The anterior part of this becomes the heart and ventral aorta, while the posterior part drains the gut. As the liver grows, it breaks up the vitelline vein into smaller and smaller channels, with fingers of liver running between them. There is thus formed a set of capillaries, separating an anterior hepatic vein, emptying into the heart, from a posterior hepatic portal vein. A portal system is one in which the blood, having passed through the capillaries of the general circulation, passes through another set on its way back to the heart. Apart from variations in the disposition of the branches coming from the gut, and one point which we shall mention later, the hepatic portal system is much the same in all vertebrates.

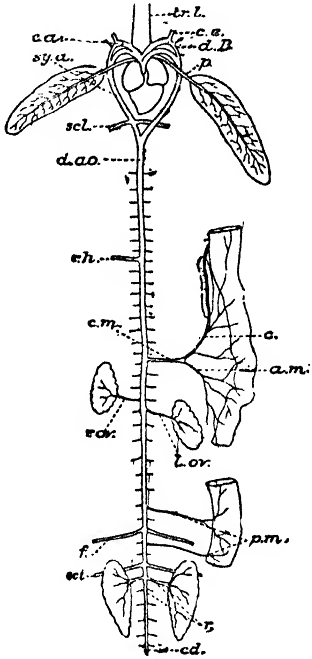


FIG. 27.44.—The principal arteries of a lizard.

a.m., Anterior mesenteric; *c.*, cœliac; *c.a.*, carotid arch; *c.c.*, common carotid; *c.m.*, cœliaco-mesenteric; *cd.*, caudal; *d.ao.*, dorsal aorta; *d.B.*, carotid duct; *f.*, femoral or external iliac; *l.ov.*, left ovarian; *p*, pulmonary; *p.m.*, posterior mesenteric; *r.*, renal; *r.h.*, right hepatic; the left hepatic is a branch of the cœliac; *r.ov.*, right ovarian; *scl.*, subclavian; *sci.*, sciatic or internal iliac; *sy.a.*, systemic arch; *tr.l.*, tracheo-lingual.

The cardinal veins run almost the whole length of the body, and are divided into anterior and posterior cardinals by a transverse common cardinal vein, or Cuvierian sinus, which carries blood from both sides into the sinus venosus. This condition

is found in embryos, and also in the adults of selachians, except that, before going into the main posterior cardinals, the blood from the posterior part of the body passes through capillaries in the kidney, making the renal portal system. In actinopterygians only part of the blood goes through this, the rest going through the posterior cardinals direct to the heart. In lung fishes and tetrapods a branch of the hepatic portal vein runs dorsally and connects with the right posterior cardinal; blood then flows

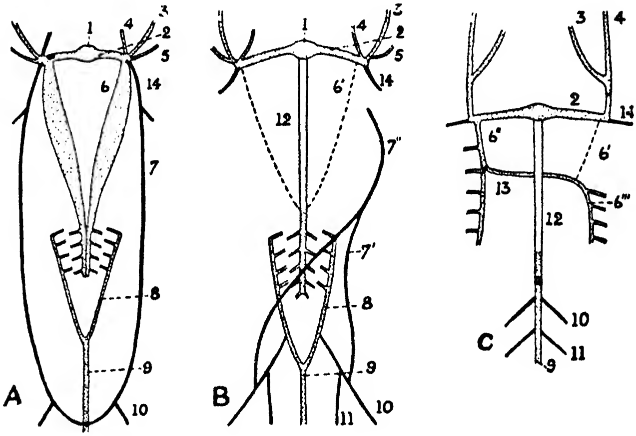


FIG. 27.45.—Diagrams of the venous system.

A, of a dogfish; *B*, of an amphibian; *C*, of a rabbit.

The primary system in grey; that of the lateral and anterior abdominal veins in black; the inferior vena cava in white. The hepatic portal system is omitted.

1, Entry to heart; 2, left superior vena cava or precaval or ductus Cuvieri; 3, left internal jugular or anterior cardinal; 4, left external jugular or inferior jugular; 5, left subscapular; 6, left posterior cardinal; 6′, position of same in a newt; in the frog the posterior cardinals are absent; in the rabbit the portion shown by dots is wanting: 6″, right azygos vein representing right posterior cardinal in a mammal; 6′, left azygos vein; 7, left deep lateral vein; 7′, pelvic; 7″, anterior abdominal, representing both deep laterals fused; 8, renal portal; 9, caudal (wanting in frog); 10, external iliac or femoral; 11, internal iliac or hypogastric; 12, inferior vena cava or postcaval; 13, junction between azygos veins; 14, left subclavian.

from the cardinal to the heart through the hepatic portal, the anterior part of which is now called the posterior vena cava. There are cross connections between the left and right posterior cardinals near the kidney, and blood from the left also flows into the vena cava. The anterior parts of the posterior cardinals become much reduced or atrophy. One of the best known relics is the azygos vein of the rabbit, which drains the intercostal region from the fifth rib backwards and empties into the right anterior vena cava. In mammals and birds the renal portal system is lost, and only the right posterior cardinal is retained, to form the posterior portion of the posterior vena cava.

The anterior cardinals do not differ greatly in the vertebrate classes, except that in mammals the original lateral veins of the head are replaced by new intracranial internal jugulars. Where the posterior cardinals have been replaced by the posterior vena cava the common cardinal no longer receives blood (except the little that comes from the azygos vein) from behind the heart, and so it is associated only with the anterior cardinals. Common cardinal and anterior cardinal of each side are now known together as the anterior vena cava, those of the right and left sides having separate openings into the auricles. The common and external jugulars represent the anterior parts of the anterior cardinals. In many mammals, such as the rabbit, there is a large ventral anastomosis between the two common jugulars, and in some, including man, the portion on the left posterior to this disappears, so that there is no left anterior vena cava and all the blood enters the auricle on the right side.

The abdominal veins are of less importance. In the dogfish two small vessels run forward in the abdominal wall and enter the sinus venosus; their homologues in the anterior region are probably the misnamed jugular sinuses which run from the head back to the heart and are seen in the dissection of the afferent branchials. Actinopterygians are very similar, but in lung fishes there is only a single median vein. In Amphibia and Reptilia not only have the abdominals fused to form a median vessel (the ventral abdominal of the frog) but the anterior portion of this opens not directly into the heart but into the hepatic portal. There is often, as in the frog, connection between abdominal and renal portal veins, so that all the blood from the posterior parts of the body has a choice of routes. In birds and mammals the abdominal veins are present only in the embryo, where they carry oxygen from the allantois and (in mammals) food from the placenta. In the adult they atrophy, and blood from the hind limbs and tail goes direct into the posterior vena cava.

In lung fishes the pulmonary veins enter the left side of the auricle; in the tetrapods they enter the left auricle, and are much the same in all classes.

NERVOUS SYSTEM

The nervous system of vertebrates, like that of all the higher Metazoa, is divisible into a central part, where impulses are

received, relayed, co-ordinated and perhaps originated, and a peripheral part which puts the central nervous system into communication with the rest of the body and so with the outside world. The central nervous system is further divided into the spinal cord, and the brain which develops from the anterior part of this. The spinal cord is much the same in all vertebrates ; an inner mass of grey matter surrounds a small canal, and is itself surrounded by white matter (p. 539). The grey matter is generally more or less H-shaped in section ; the upper parts (the dorsal columns or horns) consist of association neurons, with their cell bodies, which receive and relay sensory impulses, while the lower parts (the ventral columns or horns) consist of the cell bodies of efferent nerves. The white matter is made up of nerve fibres of various sorts carrying impulses up and down the column.

The brain is formed as an expansion of the anterior end of the spinal cord. At an early stage this begins to swell, and very soon two flexures or constrictions mark off fore, mid, and hind-brain, or prosencephalon, mesencephalon, and rhombencephalon. These, and the structures directly developed in them, constitute what is called the brain stem. Soon afterwards a lateral outgrowth, which will become olfactory lobe and cerebral hemisphere, appears on each side of the prosencephalon ; the two grow forward and may meet to form a single structure. Together with the original anterior wall of the prosencephalon, the lamina terminalis, they make the end-brain, or telencephalon, leaving the remainder of the fore-brain as the tween-brain or diencephalon or thalamencephalon. A dorsal outgrowth of the hind-brain, the cerebellum, makes it possible to distinguish an anterior metencephalon from a posterior after-brain or myelencephalon. There are thus five main subdivisions. Their cavities are called ventricles ; in the hemispheres are two lateral (or first and second) ventricles, each of which opens by a foramen of Monro into the cavity of the diencephalon, or third ventricle. This leads by a channel with the absurd names of aqueduct of Sylvius or *iter a tertio ad quartum ventriculum* to the fourth ventricle, which extends throughout the rhombencephalon and is continuous with the canal of the spinal cord. The iter is a narrow passage in mammals, but is much larger in lower vertebrates.

The chief parts of the brain are shown diagrammatically in Fig. 27.46. The roof of the tween-brain bears a number of

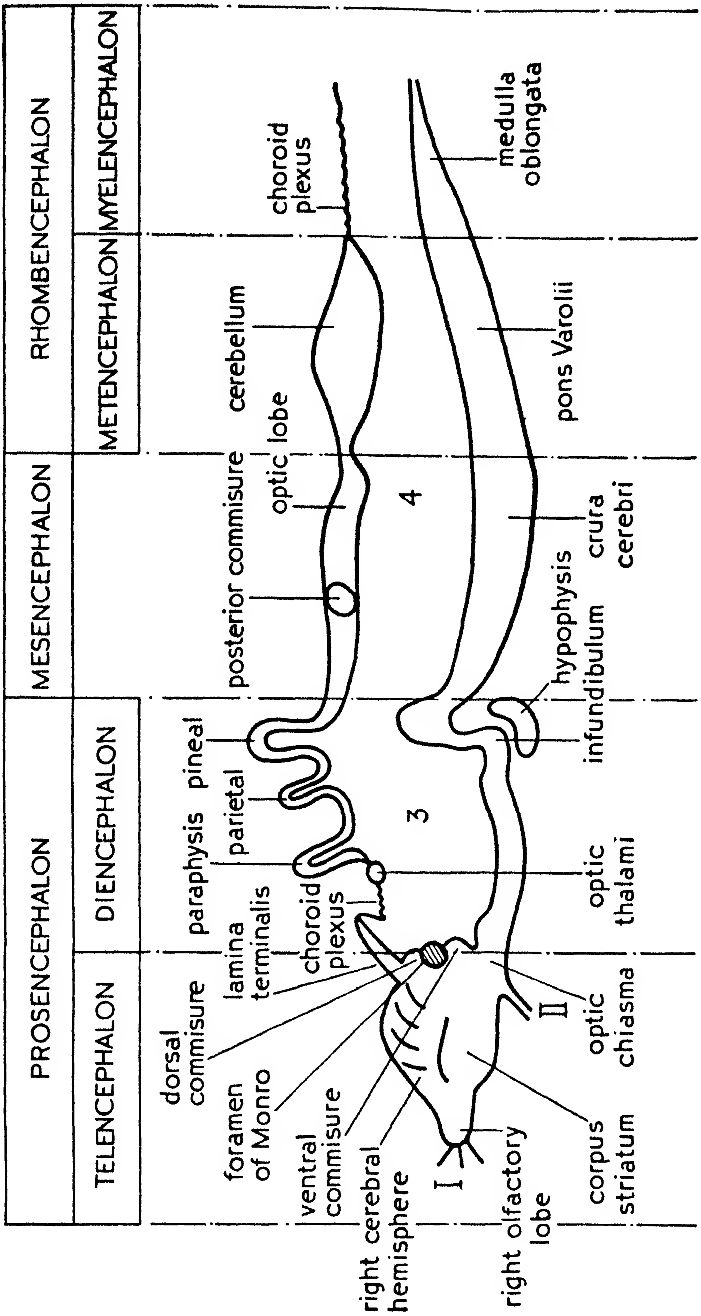


FIG. 27.46.—Diagrammatic sagittal section of vertebrate brain.

3 and 4, Ventricles ; I and II, cranial nerves

outgrowths ; the paraphysis is seldom present in adults, and it is rare for the pineal and parietal (or parapineal) bodies, both of which were originally eyes, to be well developed together. The roof between these outgrowths, like that of the myelencephalon, is thin and vascular, making a choroid plexus. From the floor of the tween-brain the infundibulum grows down to become the pars nervosa of the pituitary. Most of the other parts of the brain are thickenings in the walls. It will be seen that this diagrammatic vertebrate brain is very similar to that of the dogfish (Fig. 21.19). In the other types which we have studied (Figs. 22.41, 23.23 and 24.32) there are variations in the proportions of the parts, but no real differences of plan. In the birds, and even more in the mammals, the cerebral hemispheres are enormously expanded so that they stretch backwards and cover most of the rest of the brain. In both groups it is the grey matter which is increased, but whereas in birds it is the ventral part, or basal nucleus (=corpus striatum), in mammals it is the dorsal part or pallium, especially that part of it called the neopallium. Attempts to connect these differences with differences of behaviour, on the assumption that birds are dominated by instinct and mammals by learning, do not, however, fit the facts. Birds do show much more complex instincts than most mammals, but as a class, they show also a capacity for learning at least comparable with that of all mammals except the primates, and there is no reason why nerve connections to make this possible should not be developed in the corpus striatum. The neopallium of the primates, and especially of man, has, however, a complication reached in no birds, and on this, in a material sense, depends man's ability to reason.

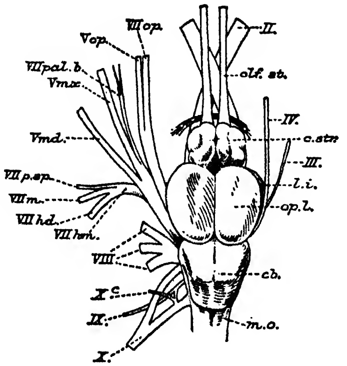


FIG. 27.47.—The brain and its nerves in a cod.

c.str., Corpora striata, two large masses or ganglia of grey matter which lie at the base of the cerebrum of Vertebrata and are here exposed because the roof of the cerebrum, which in the cod is thin and non-nervous, has been torn away; *cb.*, cerebellum ; *l.i.*, right lobus inferior ; *m.o.*, medulla oblongata ; *olf.st.*, stalk of olfactory lobe; *op.l.*, optic lobes ; *II.-V.*, *VII.-X.*, cranial nerves; *V.md.*, *V.mx.* *V.op.*, mandibular, maxillary, and ophthalmic branches of the fifth nerve ; *VII.hd.*, *VII.hm.*, *VII.m.*, *VII.op.*, *VII.p.sp.*, *VII.pal.b.*, hyoidean, hyomandibular, mandibular, palatobuccal, and ophthalmic branches of seventh nerve ; *X.c.*, cutaneous branch of the vagus nerve, from which the lateral line is innervated. The cutaneous branch of the fifth nerve is not shown.

The nerves which make up the peripheral nervous system

develop as a continuous series down the body, but it is necessary to distinguish the cranial nerves, which originate within the skull, from the spinal nerves which are outside it. Both types have a segmental pattern impressed on them by the mesoblast which they supply, and the effect on the spinal nerves is strengthened by the fact that they have to emerge between the vertebræ. The segmentation of the cranial nerves has been discussed on pages 575–6. In the lampreys the dorsal roots, coming from the dorsal columns of grey matter, remain distinct from the ventral roots, which come from the ventral columns, but in craniates the two roots of each spinal nerve join to form a mixed nerve. The cranial roots, as we have seen, remain separate. The dorsal root has a ganglion outside the spinal cord, the ventral root has one inside. The mixed nerve generally divides into a dorsal and a ventral ramus which supply the appropriate parts of the body. The ventral rami of several segments in the pectoral and pelvic regions combine to form a plexus for each limb. The pattern of this is usually highly characteristic for the species.

The fibres which make up the nerves are afferent or sensory if they carry impulses into the central nervous system, efferent or motor if they carry them out. They are also divided according to the part of the body which they serve, so that there are four main types (Fig. 27.48). Somatic sensory fibres convey impulses which are initiated by the outside world (the exteroceptive field) or by the skeletomuscular system (the proprioceptive field). They thus serve the generalised senses of touch and temperature, the special sense organs, including the ear and the acustico-lateralis system generally, and the proprioceptors which tell us of the position of our limbs, and probably also in man, help to determine our general senses of well-being.

Visceral sensory fibres convey impulses from the alimentary canal and viscera generally, and the blood vessels (the interoceptive field). The nerves of the chemical sense, including the special senses of smell and taste, probably belong here.

Somatic motor fibres convey impulses to the skeletal muscles, and are distinguished in man as most of those which are, or appear to be, under the control of the will.

Visceral motor fibres convey impulses to glands and to smooth muscle. They supply also the voluntary muscles of the gill arches and jaws, developed in association with the alimentary canal.

In mammals both sets of afferent fibres normally go in by the dorsal root, and the efferent fibres emerge by the ventral root. The more primitive arrangement, however, appears to have been for the visceral efferent fibres to use the dorsal roots ; this appears to be the case in lampreys, and in Amphibia and fishes they are found in both roots. In amniotes efferent fibres are only occasionally found in the dorsal roots of spinal nerves, but they are present

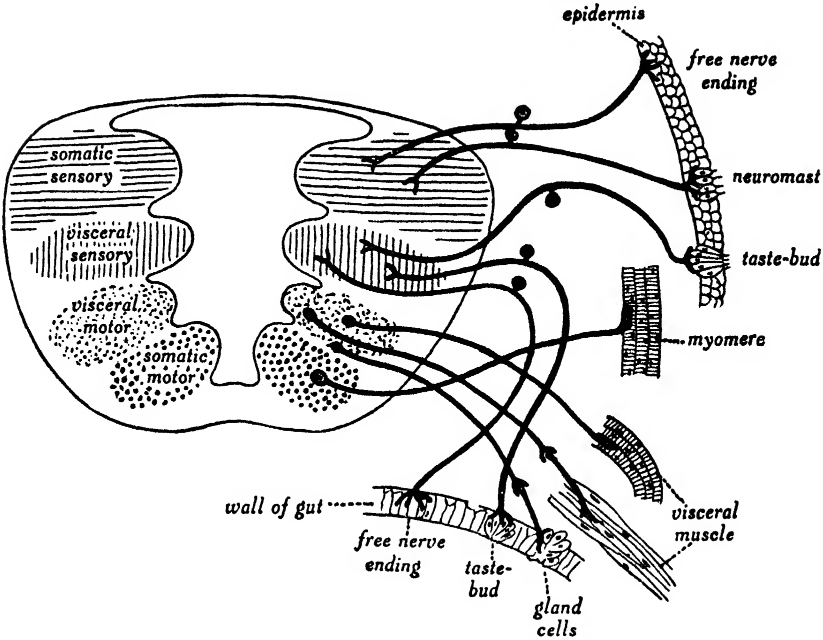


FIG. 27.48.—Diagram showing the central origin of the nerve components from the medulla, and their peripheral distribution.—From Goodrich, *Studies on the Structure and Development of Vertebrates*, 1930. Macmillan, London.

in the facial, glossopharyngeal and vagus, which are the dorsal roots of cranial nerves. Here, as in the separation of the roots, the cranial nerves of gnathostomes resemble the spinal nerves of lampreys.

The nature of the nervous impulse is basically the same in all types of fibre, and it is the same no matter what the stimulus from which it originates. A wave of change of electrical potential, accompanied and perhaps caused by a wave of change in permeability, travels in both directions from the point of stimulus. Normally, sensory nerves are only stimulated at their outer end,

motor nerves at the inner end, so that they conduct in one way only, but experimentally stimuli can be applied along their length, when it is seen that conduction takes place in both directions. The speed of conduction varies with the fibre and with the temperature; the fastest mammalian fibres conduct their impulses at about 100 metres per second. At the nerve-muscle junction and at a synapse the nerve fibre liberates a chemical

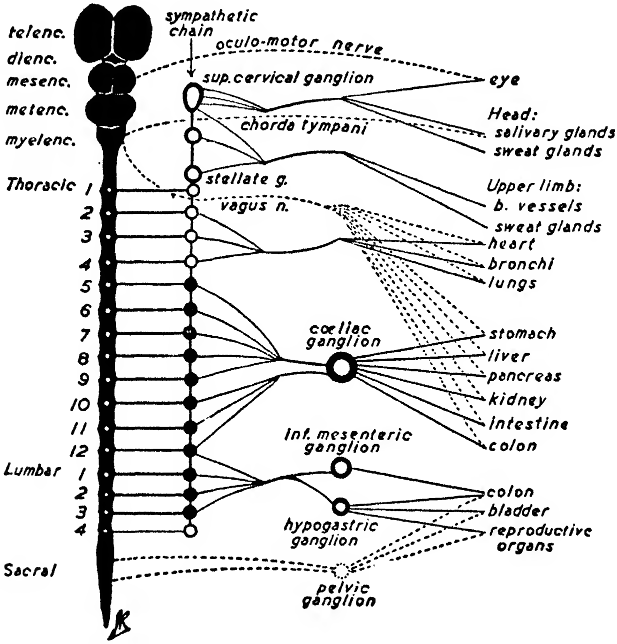


FIG. 27.49.—Diagram of the autonomic nervous system of higher vertebrates.—From Thomson.

The sympathetic system is indicated by unbroken lines, the parasympathetic by broken lines. Where ganglia are shown solid black a sympathetic path is continuous, in the others the pre- and post-ganglionic nerves are in association through synapses or relays.

substance which causes response or starts a new impulse in the next fibre; in somatic nerves this is acetylcholine, but, as described below, there are differences in the autonomic system.

The visceral motor system, excluding that part of it which innervates the branchial and other voluntary musculature, has some peculiarities of structure and behaviour, and is known as the autonomic system. Its fibres differ from those of the ordinary peripheral nerves, in that a single one does not reach directly to the organ which it is going to affect. Sooner or later each fibre from the central nervous system comes to a synapse, and its

impulse is relayed to another neuron. The bodies of these secondary neurons are collected into special ganglia, many of which are a long way from the central nervous system. The post-ganglionic fibres (the axons of the second neurons) are usually non-medullated, and make up the autonomic nerves in the limited sense ; the preganglionic fibres are the axons of the connector neurons, running from the central nervous system to autonomic ganglia.

In cyclostomes the autonomic system is not well differentiated, but in all gnathostomes it is built on much the same plan ; the following description applies primarily to mammals. Physiologically it is divisible into two, but anatomically into four. The sympathetic system (in the strict sense ; sometimes the term is used as a synonym for the autonomic system) comes from the spinal nerves in the thoracic and lumbar regions (Fig. 27.49). The axons of the connector neurons emerge with the ventral roots, and then run as white rami communicantes to a segmental series of lateral ganglia on each side of the dorsal aorta ; the ganglia are connected by branches of the connector neurons so that they form a double chain. This is the sympathetic system of the frog as it is usually dissected. The chain is continued forwards into the neck where it forms anterior and posterior cervical ganglia, and backwards into the sacral region. In each segment post-ganglionic fibres run as grey rami communicantes to join the appropriate spinal nerves, and supply the sweat glands, erector muscles of the hair, the larynx and the heart, while others run to the viscera, urethra, bladder and copulatory organs. A fibre may run through more than one ganglion, but there is only one synapse between the outflow from the cord and the effector. All sympathetic nerves are adrenergic ; that is, they act on their effectors by liberating a substance called sympathin, which is closely similar to adrenaline.

The parasympathetic system, by contrast, is cholinergic, that is, it acts by liberating acetylcholine, just as do the somatic motor nerves. It has three outflows from the central nervous system ; through the oculomotor nerve to the ciliary ganglion, and so to the sphincter of the iris and the ciliary muscle ; through the facial, glossopharyngeal and vagus nerves ; and through the spinal nerves of the sacral region. The branches from the facial and glossopharyngeal supply the salivary glands, and those from the vagus go to the heart, lungs and alimentary canal as

far back as the posterior end of the small intestine; they form the plexus of Auerbach and the plexus of Meissner. The sacral outflow sends branches to the large intestine, bladder and copulatory organs. Both systems thus supply smooth muscle and glands all over the body, and they are largely antagonistic in their effects; for example, the sympathetic branch from the

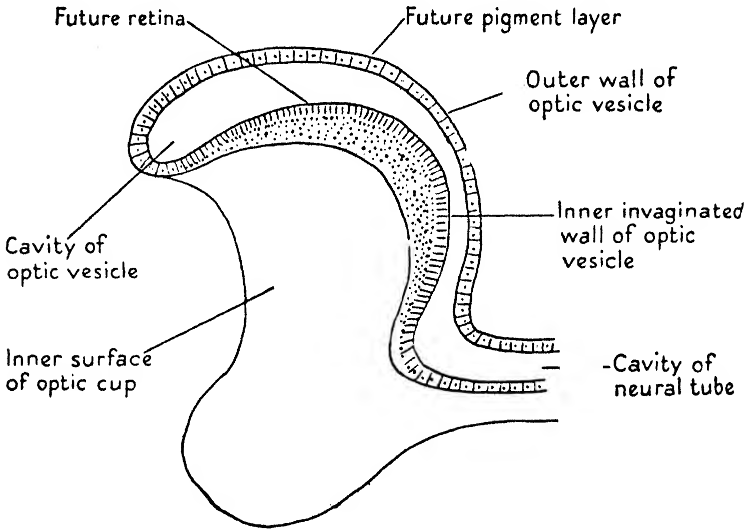


FIG. 27.50.—A vertical section of the developing optic cup, showing how the sensitive cells of the retina come to lie on the outer surface.—From Willmer. Bourne, *Cytology and Cell Physiology*, 2nd edition, 1951. Clarendon Press, Oxford.

inferior cervical ganglion to the heart accelerates it, while the parasympathetic branch of the vagus (the depressor) slows its beat; sympathetic fibres cause contraction of the arteries of the penis, parasympathetic fibres their dilatation, and so the erection of the organ.

The eye is formed largely from the brain. As the neural plate (p. 653) rolls up, two projections in the region of the midbrain grow out laterally, roll up, and at the same time become hollowed out to form first a hollow-walled cylinder and then a cup. The cavity between its walls (which later disappears) is continuous through the optic stalk with the third ventricle, and a chink left where the cup is not quite complete is the choroid fissure. (Figs. 27.50 and 27.51). A small area of ectoderm enclosed by the rim of the cup sinks in and dies, and in doing so induces the formation

of the lens from the edge of the optic cup. The cup produces also the iris and its musculature, and the zonule of Zin which suspends

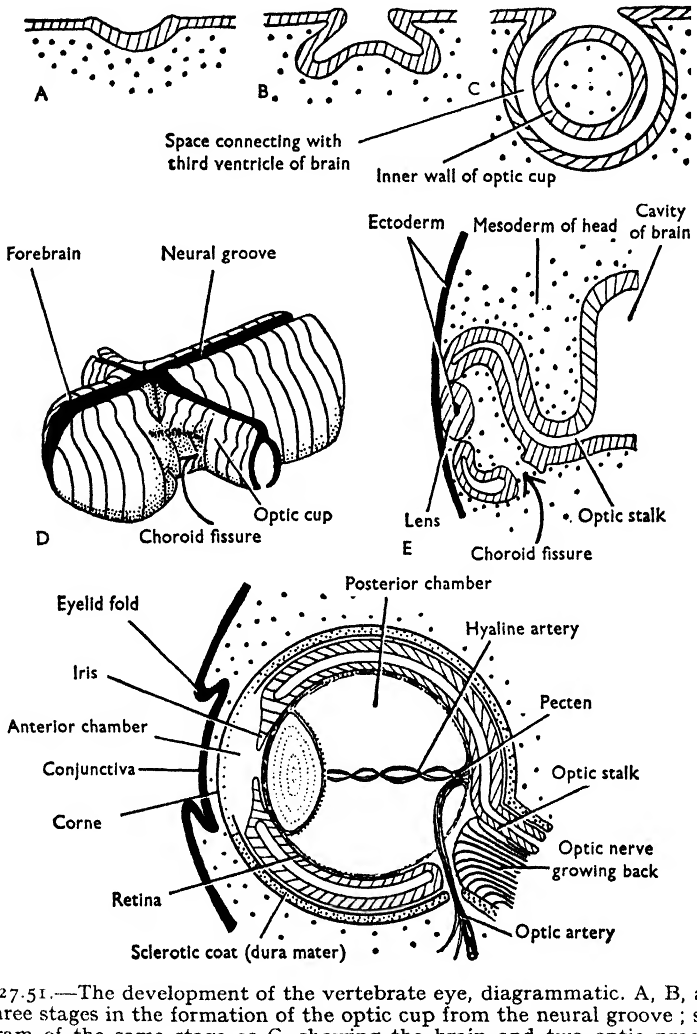


FIG. 27.51.—The development of the vertebrate eye, diagrammatic. A, B, and C, three stages in the formation of the optic cup from the neural groove ; stereogram of the same stage as C, showing the brain and two optic processes ; transverse section of the same stage : the dead ectodermal evocator may be seen in the lens ; E, a section of a well-established eye, with processes from the retina forming the optic nerve.

the lens so that the cavity of the cup is divided into anterior and posterior chambers. The inner wall of the cup differentiates into the layers of the retina, the outermost of which grow back along

the optic stalk to the brain as the optic nerve. The cornea is formed from ectoderm, the humours probably from mesenchyme, and the eye is complete.

The variations of the eye in the different classes of vertebrate lie largely in the histology of the retina and in the method of

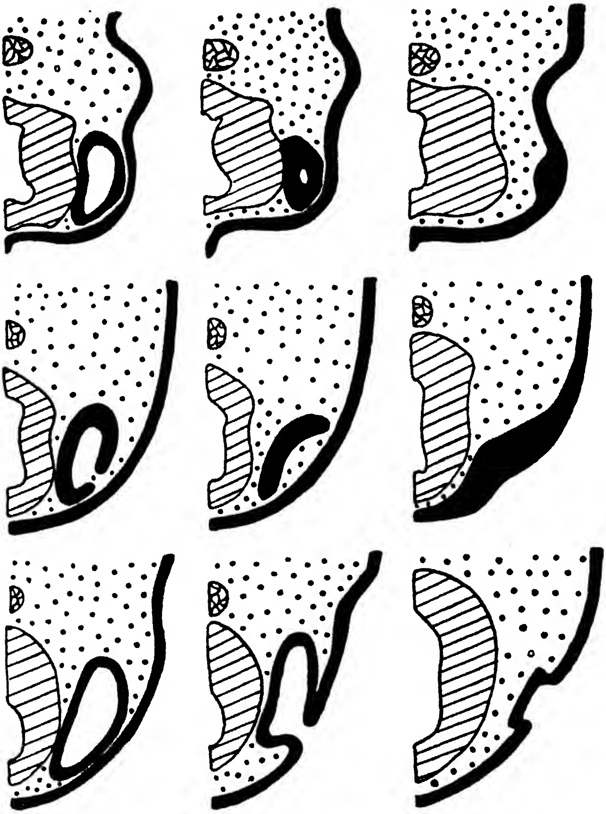


FIG. 27.52.—Diagrams of the mode of formation of the ear placode in vertebrates. Upper row, chick ; middle row, frog ; lower row, teleost. Three stages are shown for each.

accommodation. Birds have developed the simple eye almost to its limit, with extreme discrimination, good colour sense, and almost no spherical aberration, but they have little stereoscopic vision.

The main parts of the ear are derived from the brain, but the sequence of events is different in different vertebrates. In birds (Fig. 27.52) a flattening of the ectoderm on each side of the hind

brain, called the auditory placode, begins to sink into the underlying mesoderm, where it expands and becomes cut off from the surface as a hollow auditory vesicle. In Amphibia (Fig. 27.52) the placode drops in as a plate and rolls up to enclose some mesoderm, which dies, leaving a cavity. In the teleosts (Fig. 27.52) the placode thickens on the surface, drops in, and then a cavity appears within it. However the auditory vesicle may be formed, from it are developed the parts of the inner ear. These are the semicircular canals (two vertical and one horizontal), all of which open into the utriculus, a sacculus opening out of the utriculus, and attached to it a smaller chamber, the lagena. In the amniotes, and especially in the mammals, an outgrowth of the lagena forms a much larger structure, the cochlea, which is the organ of hearing. Most of the ear is concerned with balance. Nerve fibres grow in from the eighth cranial nerve to form sense cells on the inner surface. The whole inner ear comes to be covered with the membranes of the brain, and the perilymph which surrounds it is continuous, through the ductus cochlearis, with the liquid surrounding the brain. The labyrinth is almost completely enclosed in cartilage or bone derived from the auditory capsule.

The middle ear develops from the first gill pouch (the spiracle of fishes), so that it is lined with endoderm and communicates with the pharynx by the Eustachian tube, which in many reptiles is multiple. Across it runs the columella auris, or, in mammals, the auditory ossicles (p. 594). The ear drum or tympanum, which is originally part of the outer surface of the body (and remains so in Amphibia and Reptilia), consists of ectoderm with mesoderm and endoderm below it.

THE EXCRETORY SYSTEM

The excretory system of vertebrates is derived from a series of paired segmental cœlomic tubules, which may be known collectively as a holonephros. It is customary and convenient to divide this into three sections, by time of development and position in the body, but there are no fundamental differences between them. Most anterior and earliest to appear is the pronephros, behind this and a little later is the mesonephros, and further back and later still is the metanephros, which is only well developed in the amniotes The tubules of all these divisions

have the same basic structure, and it has been shown experimentally that their physiology is also essentially the same.

All the tubules are derived from a segmented portion of the mesoderm, which lies between the somites (or myotomes) and the lateral plate. On each side of each somite an intermediate cell mass becomes organised as a hollow nephrotome, containing a cavity, the nephrocœle; this is part of the cœlom (p. 187) and early communicates with the myocœle, and for much longer with the splanchnocœle. One part of its wall grows out dorsally or laterally as the excretory tubule, and another is pushed in as Bowman's capsule, the wall of which becomes thin and into which the blood vessels of the glomerulus grow. The tubules of adjacent segments communicate so that they have a common duct, and this grows back as the segmental duct to the cloaca. The opening of the tubule into the cavity of Bowman's capsule is the nephrocœlostome (the alternative name nephrostome may cause confusion with a structure of different nature in annelids) and the opening from Bowman's capsule to the splanchnocœle is called the peritoneal funnel. The resulting simple structure is shown in Fig. 27.53 A.

This arrangement of tubules is found very nearly for the full length of the body in the hagfish *Bdellostoma*, and in the Gymnophiona. The organ in these animals used to be described as a functional pronephros, but it is better to think of it as an undifferentiated holonephros; there are differences between the anterior and posterior tubules, but any change is gradual and it is impossible to separate one part rigidly from another. A pronephros, in the sense of an anterior set of tubules which can be distinguished from the rest, is found only in those vertebrates with a larval stage, namely, Dipnoi, Crossopterygii, Actinopterygii and Amphibia. In all these it is the larval excretory organ, developed early in life; it may be seen in a careful dissection of the tadpole (Fig. 27.54). It generally atrophies, but is functional in the adults of a few teleosts (e.g. *Fierasfer*). In amniotes it is represented, if at all, only by a few anterior rudimentary tubules, but its duct persists in the female of all vertebrates as the oviduct.

Behind the region of the pronephros the nephrogenic part of the mesoderm is often condensed or not segmented, but the general development of the tubules is basically the same, except that it is common for secondary and tertiary tubules to bud off from the primary ones. This part of the kidney, the mesonephros,

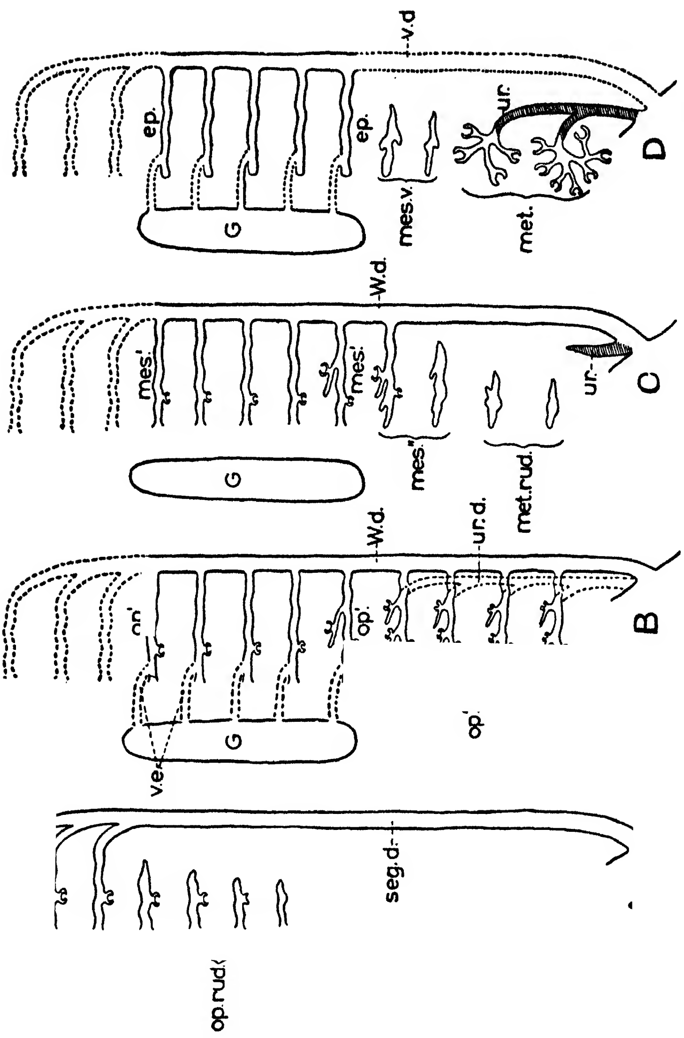


FIG. 27·53.—A diagram of the kidney tubules and ducts of Vertebrata.

A., Condition in larva of fishes and amphibians (pronephric tubules shown with separate glomeruli.) *op. rud.*, developing rudiment of mesonephros; *pn.*, pronephros; *seg.d.*, segmental duct. *B.*, Condition in adult fishes and amphibians. *G.*, gonad; *op'.*, part of the mesonephros which in the male is connected with the testis; *op''.*, part of the mesonephros which is purely urinary in both sexes; *ur.d.*, urinary duct of male dogfish and newt; *v.e.*, vasa efferentia; *W.d.*, Wolffian duct. *C.*, Condition in the embryos of reptiles, birds, and mammals, after the degeneration of the pronephros. *G.*, gonad; *mes'.*, part of the mesonephros which in the male becomes connected with the testis; *mes''.*, rest of mesonephros; *met. rud.*, rudiment of metanephros; *ur.*, rudiment of ureter; *W.d.*, Wolffian duct. *D.*, Condition in the adult of reptiles, birds, and mammals. *ep.*, in male, epididymis, in female a vestige known as epoophoron; *G.*, gonad; *mes.v.*, vestige of hinder part of mesonephros, known in male as paradidymis, in female as paroophoron; *met.*, metanephros (possibly formed by the branching of one tubule only); *ur.*, ureter; *v.d.*, vas deferens (in male only).

is the functional kidney of nearly all adult anamniotes, including the elasmobranchs. Its duct, the mesonephric or Wolffian duct, is formed in the same way as the pronephric or holonephric duct. It is also active in the embryos of reptiles, birds and mammals, and in reptiles, monotremes and marsupials for a short time after birth. Two related tendencies are to be noted in it: towards separation into anterior and posterior portions, and towards association with the gonads. In all gnathostomes except teleosts there is in the male an anterior part which ceases to be excretory and becomes sexual in function, and helps to convey

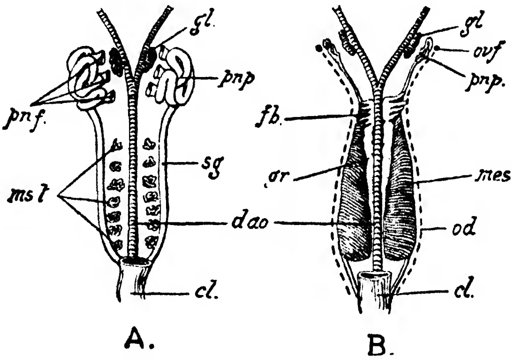


FIG. 27.54.- -Diagrams of the development of the excretory system of the frog.- From Bourne.

A., The system of a tadpole about 12 mm. long, showing the pronephros and origin of the mesonephric tubules; *B*, the system at the end of metamorphosis. The broken line represents approximately the position of the strip of peritoneal epithelium which gives rise to the oviduct.

cl., Cloaca; *d.ao.*, dorsal aorta; *f.b.*, fat body; *gl.*, glomus; *g.r.*, genital ridge; *mes.*, mesonephros; *ms.t.*, mesonephric tubules; *od.*, oviduct; *ovf.*, position of oviducal opening; *pn.f.*, pronephric funnels; *pnp.*, pronephros; *sg.*, segmental duct (the line points to the part which becomes the Wolffian duct).

the sperms to the exterior. The Wolffian duct is also a sexual duct, but in some, such as the toad and dogfish, there is a more or less complete split of the ducts into sexual and excretory parts. This tendency is carried further in the amniotes. Here a new duct, the ureter, grows forward from the mesonephric duct near its lower end, and round the head of this new channel a mass of unsegmented nephrogenic tissue forms a complex series of branched tubules, which never open to the splanchnocœle. This is the metanephros, and the ureter is the metanephric duct. It is probably best not to use these terms except for structures in the amniotes, but it must be recognised that many anamniotes have a closely comparable arrangement which cannot formally be separated. The terms vas deferens and ureter may

justifiably be used for separated portions of the Wolffian duct which are respectively sexual and excretory in function.

All the ducts open posteriorly at first into the alimentary canal, and this arrangement persists in the fish and amphibians, and with some modification in reptiles and birds, so that there is a cloaca. In mammals the front wall of the allantois grows back and separates a dorsal rectum from a ventral urogenital sinus, which thus becomes separated from the gut and has its own opening to the exterior. Internally it bears, from in front backwards, the opening of ureters, bladder, Wolffian ducts in the male, and (just on its edge) Müllerian ducts in the female. The neck of the bladder (derived from the proximal part of the allantois) becomes constricted, and the ureters open into it just

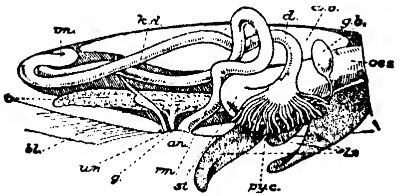


FIG. 27.55.—A semi-diagrammatic view of the contents of the abdominal cavity of a male cod which has been opened on the right-hand side.

a.b., Air-bladder; *an.*, anus; *bl.*, bladder; *d.*, duodenum; *g.*, genital opening; *g.b.*, gall-bladder; *im.*, ileum; *kd.*, kidney duct; *lr.*, liver; *œs.*, œsophagus; *py.c.*, pyloric cæca; *rm.*, rectum; *st.*, stomach; *t.*, testis; *ur.*, urinary opening.

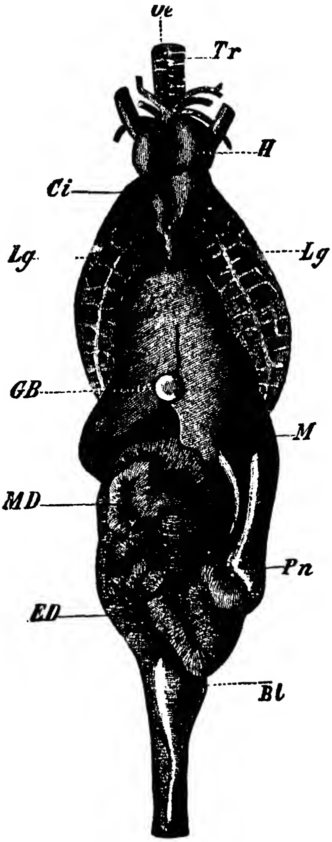


FIG. 27.56.—The viscera of the sand lizard (*Lacerta agilis*), in their natural relations.—From Weidersheim.

Bl., Bladder; *Ci.*, inferior vena cava; *ED.*, rectum; *GB.*, gall-bladder; *H.*, heart; *Lg.*, lungs; *M.*, stomach; *MD.*, small intestine; *Oe.*, œsophagus; *Pn.*, pancreas; *Tr.*, trachea.

above. The Müllerian ducts fuse where they pass down the septum between the urogenital sinus and the rectum (the broad ligament) and so form the uterus. In the male the openings of the urethra

and Wolffian ducts become progressively enclosed so that there is finally a single orifice at the end of the penis.

Table X and Fig. 27.53 show in summary form the distribution of types of kidney in the vertebrates.

TABLE X

THE KIDNEY IN GNATHOSTOMES

		Anamniota Male	Anamniota Female	Amniota Male	Amniota Female
Pronephros	Organ	Functional in larvæ except elasmobranchs, and in a few adult teleosts		Vestigial only	
	Duct	'Sperm Sac'	Oviduct	Uterus masculinus (in part)	Oviduct
Mesonephros	Organ	Upper: Sexual; Lower: Excretory	Upper: Aborts; Lower: Excretory	Functional in embryos: Retia and vasa efferentia; epididymis	Functional in embryos: Paroöphoron
	Duct	Excretory duct; Vas deferens	Excretory duct	Vas deferens	Aborts or vestigial (Gärtner's canal)
Metanephros	Organ			Adult Kidney	Adult Kidney
	Duct			Adult Ureter	Adult Ureter

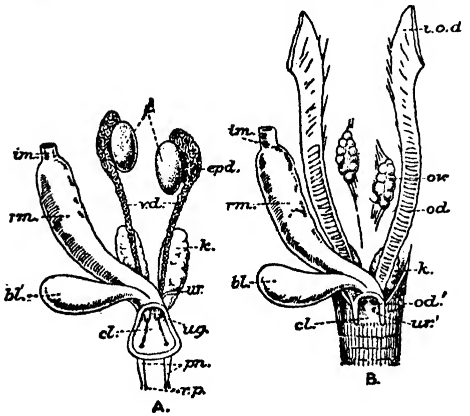


FIG. 27.57.—The urinary and genital organs of a lizard (*Lacerta*).

A, Male; *B*, female.

bl., Bladder ; *cl.*, cloaca ; *epd.*, epididymis ; *i.o.d.*, internal opening of the oviduct ; *im.*, ileum ; *k.*, kidney ; *od.*, oviduct ; *od'.*, external opening of oviduct ; *ov.*, ovary ; *pn.*, penes ; *r.p.*, retractor muscles of the penes ; *rm.*, rectum ; *t.*, testes ; *ug.*, urogenital opening ; *ur.*, ureter ; *ur'.*, opening of ureter ; *v.d.*, vas deferens.

28

EMBRYOLOGY

Hitherto we have been concerned almost entirely with the anatomy and physiology of adult animals, but we must now consider how these adults develop from the cells in which they have their origin. The study of this development is embryology.

Almost all individuals arise from an ovum and a spermatozoon as a result of syngamy (p. 4). Most eggs are more or less spheroidal in shape, and many of them contain large amounts of the inclusions called yolk. In the strict sense this consists of lecithins, substances formed from glycerol, two aliphatic acids (not necessarily the same) and an amine-substituted phosphoric acid, but the word is also used by embryologists in a broader sense to include other foodstuffs such as oil. Yolk is used to provide both energy and substance for the developing embryo, and, as we shall see later, its presence, especially in large quantities, has profound effects on the method of development. The last two divisions that prepare the egg for syngamy are very important and are known as maturation divisions. The nuclear changes in these are described on pages 700–2. The penultimate division is cytoplasmically very unequal, one of the daughter cells being the first polar body, which consists of little but nuclear material (Fig. 28.2 C). It may or may not divide again, but in any case it gives rise to no part of the adult. At the second maturation division, which usually takes place after fertilisation has begun, a similar second polar body is given off.

The sperms of most animals consist of a subspherical head containing the nucleus and a little cytoplasm and a long tail which has the typical structure of a flagellum (p. 40) ; head and tail are joined by a short middle piece, which contains mitochondria. A diagrammatic representation of a mammalian sperm and the forms of some others are shown in Fig. 28.1. Sperms of nematodes and arthropods, two phyla which are entirely without cilia and flagella, have atypical structure and have no tails.

Fertilisation has two aspects : the penetration of the sperm into the egg and the fusion of the male and female nuclei ; these last, since they differ from the nuclei of ordinary cells in being haploid, are sometimes called pronuclei. Once the sperms have

been placed by the male parent in the vicinity of the egg, their large number and their motility, often and perhaps always increased by substances liberated by the egg or the female parent, ensure that many of them reach the egg. The method of penetration is obscure, but it seems to depend in part on chemical substances associated with the specialised anterior end of the sperm, the acrosome. The tail is left outside (except in mammals) and

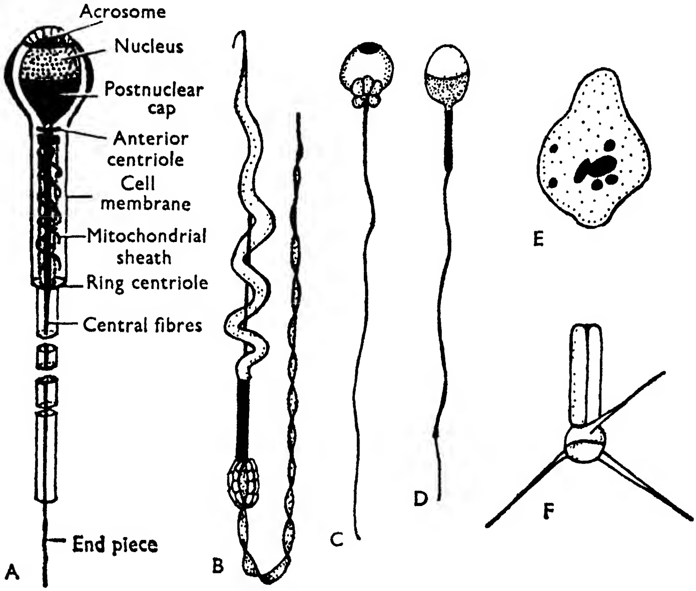


FIG. 28.1.—Spermatozoa. *A*, diagram of mammalian sperm; *B*, sperm of elasmobranch (ray); *C*, of *Branchiostoma*; *D*, of man; *E*, of *Ascaris*; *F*, of lobster.—Based on Nelsen, *Comparative Embryology of the Vertebrates*, 1953, Blakiston, New York.

head and middle piece, or structures derived from them, travel through the cytoplasm of the egg towards its nucleus. Homologous chromosomes from the two gametes come together and the zygote nucleus is formed. The middle piece forms part of the sperm aster, a centrosome-like body which escorts the sperm nucleus, forms a spindle during nuclear fusion, and may remain for the first division.

In some animals many sperms penetrate the egg, in others only one does so, and in all a barrier to further penetration is formed at some stage. This consists in part of a fertilisation membrane, which appears round the egg sometimes within a minute and sometimes up to four hours after the entry of the first

sperm; in some species it is simply the original bounding or cytoplasmic membrane of the egg (called rather badly the vitelline membrane, even when little yolk is present), which has been raised up and made distinct, and has no doubt undergone other changes. Some of the events of fertilisation are shown in Fig. 28.2.

It was not until the second half of the nineteenth century, when the process of fertilisation became clearly established and improved compound microscopes showed the chromosomal structure of the nucleus, that any worthwhile theory of embryology could be put forward. It is now clear that development is a process of epigenesis, that is of the appearance of new structures that have no previous existence. To say this explains nothing, but it directs attention to what are, in part, soluble problems. We begin with an egg with components (chromosomes, mitochondria, cortex, and so on) little different in form from those of any other cell, but with an organisation that gives it the capacity to develop, as other cells (with rare exceptions in animals) cannot do, into a whole organism. The study of how this organisation originates and is maintained, how the parts react on each other and are affected by the environment, so that in the end a mature animal producing another generation of gametes is obtained, is the task of embryology. In the account that follows we have made an attempt to combine the experimental approach, now over half a century old, with the more formal description of classical embryology.

The first traces of organisation can be seen in the ripe egg as it leaves the ovary, for although it is usually spherical it is not radially symmetrical. The spindle for the first maturation division divides the cell into two parts, and the point at which the first polar body is extruded makes one of the poles of the sphere. Although in some eggs yolk is scattered throughout the cytoplasm, in others it is concentrated in one half of the sphere. When this is so, the nucleus is in the other half, and as a rough approximation is placed at the centre of gravity of the cytoplasm excluding the yolk. The polar body is therefore discharged from the surface of the non-yolky hemisphere. We can thus define the poles: the cytoplasmic pole where the polar body is formed and there is little yolk, and its antipode, the yolky pole.[1] This polar axis is determined by the position of the egg in the body; in the frog,

[1] These are often called animal pole and vegetative (or vegetal) pole respectively, but as these terms are misleading they are best abandoned.

for example, the yolky pole is that which is deeper in the ovary.

The distribution of the yolk may be said, by analogy with the

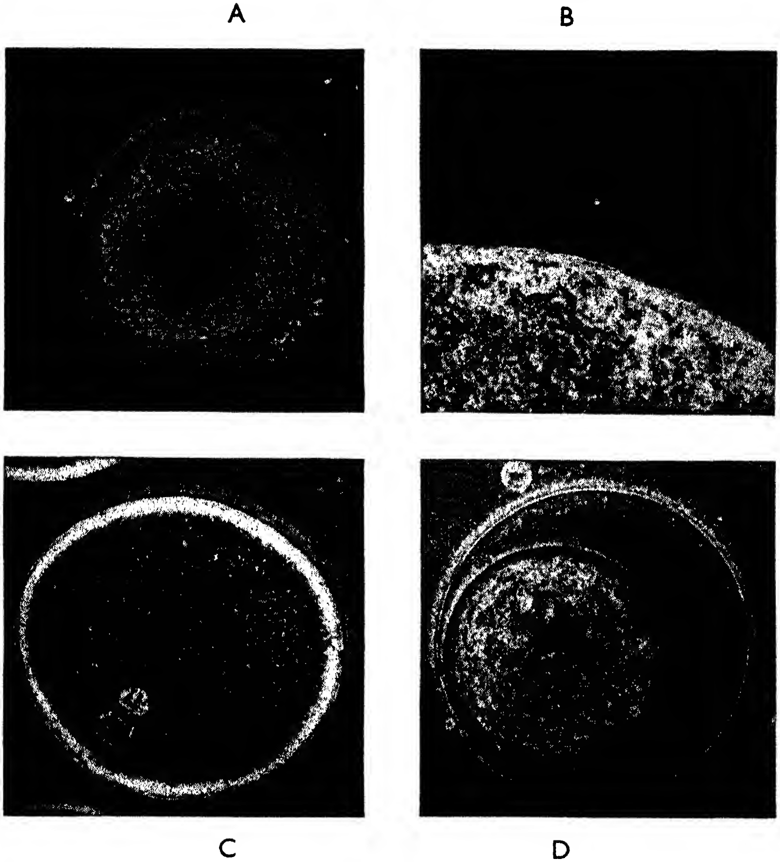


FIG. 28.2.—Fertilisation in the starfish *Asterias*. *A*, egg before fertilisation : the dark area in the centre is the nucleus, and sperms can be seen in the jelly surrounding the vitelline membrane. *B*, a higher magnification, showing the fine filament from the cortex of the egg at the point where a sperm is entering ; *C*, the first polar body is about to be extruded : the light areas are the nuclei ; *D*, after fertilisation : the dark patches are the chromosomes of egg and sperm, and the outer circle is the fertilisation membrane raised from the surface of the egg.

earth, to define the latitude of the sphere. Longitude is generally determined by the point of sperm entry, which divides the egg into right and left halves, and so may be said to mark the meridian. The point of sperm entry is determined in some species by the position of the egg in the ovary but in others it is random.

CLEAVAGE

Since the egg is a single cell and the adult is multicellular an important part of development consists of cell-divisions, and the early few of these are known as cleavage (or, badly, segmentation). At its simplest, when it is complete and holoblastic, it consists of a series of equal and simultaneous divisions leading to an increase in the number of cells by powers of two ; this is well seen in *Branchiostoma* (Fig. 28.6), and in sea urchins, which are especially good material as ripe adults can be obtained from marine laboratories in the spring and the whole process of fertilisation and cleavage watched under the microscope. The first cleavage is vertical, and passes through the point of sperm entry, while the second is also vertical but at right angles to the first. The third is horizontal and equatorial. Synchronous divisions follow until there are, usually, 64 cells, after which irregularity sets in.

The discrete cells of an early embryo are called blastomeres ; they have surface tension and tend to be spherical, so that they do not easily pack together, and in most embryos at the eight-cell stage they pull apart and leave a space in the centre (Fig. 28.3 B). Such a space is called a blastocœle, and any embryo possessing one is a blastula. This name is also applied to comparable stages in embryos where no blastocœle is clearly present ; where cleavage produces a solid mass of cells, as in the mammal (p. 668) the stage is called a morula.

After the blastula is fully formed cell-division is accompanied by cell movements, and in the simple case the hollow sphere is converted into a slightly elongated two-layered structure, the gastrula (Fig. 28.9). The formation of this begins in the sea urchin with a patch of cells opposite the original point of sperm entry putting out pseudopodia towards the blastocœle and pulling in a dent on the embryo's surface. From this dent complicated cell-movements, called morphogenetic, lead to the production of the gastrula. It has a new cavity, the primitive gut or archenteron, and the opening of this to the outside world, at first wide and then narrow as it contracts like the mouth of a string purse while the cells roll over its rim, is called the blastopore.

The formation of a gastrula is gastrulation, but this term is used also in a more general sense for the cell movements that lead to the primitive body-form of the animal, even when no strict gastrula is present as such. In this sense the term is best confined

to the vertebrates, where although the presence of yolk distorts the pattern of cell movements, the homologies are fairly obvious.

In the typical gastrula there are two, or sometimes three, layers of cells, and in other early embryos, such as that of the chick (Fig. 28.22) similar layers can be seen. These are the germ layers, and the outermost is epiblast, the inner, making the wall of the gut, is hypoblast, while the one between them, if present, is mesoblast. Epiblast gives rise to ectoderm, which includes

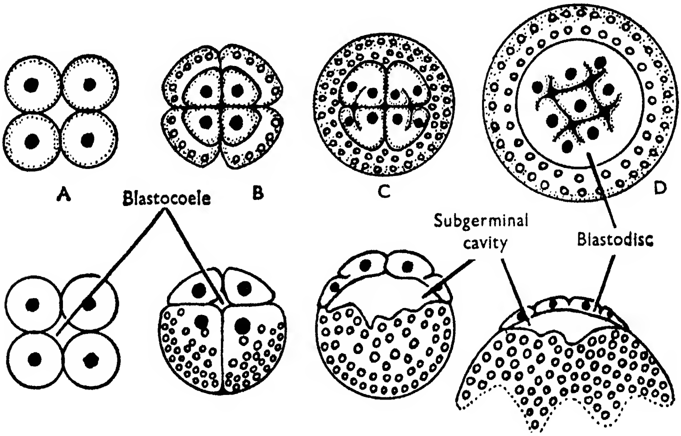


FIG. 28.3.—Diagrams of 8-celled embryos. Upper row, viewed from the cytoplasmic pole, lower row, sagittal sections. *A*, echinoderm ; yolk distributed through egg ; *B*, frog, moderate amount of yolk at one pole of egg ; *C*, fish, much yolk ; *D*, reptile and bird, much yolk.

the outer part of the skin of vertebrates (p. 531), and nervous tissue and its derivatives including the neural crest (p. 654) ; the hypoblast gives endoderm, which consists only of the epithelium of the midgut and its derivatives ; and the mesoblast gives mesoderm, which constitutes the bulk of the body—muscles, blood system, bones and kidneys. There is however no absolute constancy of derivation of a particular tissue from one germ layer rather than another, and the differences between them are probably not fundamental, so that the terms should be used in a descriptive sense only.

DETERMINATION

The appearance of specialisation while development goes on is accompanied by a loss of the egg's general power of giving

rise to all types of tissue, for although a small group of the interstitial cells of *Hydra* can grow into a complete individual, and although much regeneration is possible in animals such as turbellarians and worms, in most animals reproduction takes place only through the egg, and regeneration is very limited in amount and practically confined to wound-healing. When the egg or the embryo has lost its general power of development, so that it can give rise only to a limited range of types of cell, it is said to be determined or organised.

This determination takes place in the nematode egg even before syngamy, and cases have been reported where isolated parts of the egg have developed into perfect parts of the adult or larva as if the rest had been present. This is accompanied by an extraordinary constancy in the number of cells in each organ, which is the same throughout all the individuals of a species. More usually, determination begins at syngamy or during cleavage. As the gametic nuclei fuse there is often a redistribution of material shown by cytoplasmic streaming, the movement of pigment and yolk granules, and the breakdown of the cortical granules usually present in the outer part of the cytoplasm. In the echinoderms and vertebrates a separated early blastomere (such as $\frac{1}{2}$, $\frac{1}{4}$, or even $\frac{1}{8}$, according to the fraction of the total embryo that it makes) may develop into a perfect individual, though usually a small one ; the movements have not led to the distribution of different types of cytoplasm in different cells, and cleavage is indeterminate. In *Branchiostoma* and the tunicates separated blastomeres will not develop, there has been separation of material (which in the tunicates is visible) and cleavage is determinate or mosaic. Determinacy is especially characteristic of the spiral cleavage found in worms and molluscs (p. 676).

That cell walls are not essential for a considerable degree of specialisation is shown by the complicated internal structure of many Protozoa, and under certain circumstances the egg of the polychæte worm *Chætopterus* can develop into an almost perfect larva without any cleavage. Cell walls are concerned with size rather than with specialisation (though no doubt they assist in this), so that cleavage may be considered as being parallel to but not an essential part of the organisation of the embryo.

As soon as determination has taken place one may be able to point to a particular part of the embryo as being destined to give rise to a particular part of the adult ; the connection is shown

experimentally by surgery—excision of the part from the embryo leads to the absence of the corresponding part from the adult. Where determination is late, as in most vertebrates, it is a continuing process, and such an exact correspondence cannot be established. Instead, one can say that *under normal circumstances*, a given part of the embryo will give rise to a particular part of the adult. Such correspondences are generally shown by applying stains to parts of the embryo and following the fate of the coloured patches in individuals killed and sectioned at different

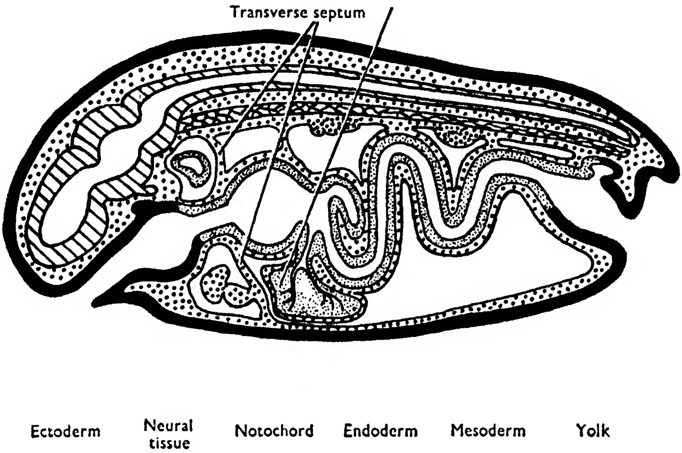


FIG. 28.4.—A diagrammatic sagittal section of a vertebrate embryo, to illustrate fate-maps. The key of shading will be used in later diagrams.

intervals of time. Students of geography will know that a map of a continent divided into countries can be distinctively coloured, with no two countries of the same colour touching, by the use of four colours only, and in the same way a solid body can be distinctively marked in seven colours. In tracing embryos forward it is convenient to deal with only one or two colours at a time, but alternatively we can start by colouring the whole later embryo with its seven colours (Fig. 28.4) and imagine them traced backwards in time, like a cinematograph film put through the projector the wrong way. The result will show, when we get to the blastula, the areas which will normally give rise to the tissues that we coloured. It will be what is called a presumptive or fate map of the embryo. A fate map for the frog and the later stages are shown in Figs. 28.4, and 28.14. In these and similar

diagrams we have used various forms of shading, but the reader is recommended to colour the figures according to the following key :

Ectoderm :	black, as used by the printer (blue is the conventional colour).
Mesoderm :	red.
Endoderm :	green.
Nervous system	violet.
Notochord :	orange.
Yolk :	brown.
Spaces :	uncoloured.

Experimental interference with the cells of the blastula and later embryos shows that their fate is finally determined by influences coming from other usually adjacent tissues ; such tissues are called organisers, and examples are discussed on later pages, particularly in the account of the development of the frog. The action of an organiser is known as induction.

DEVELOPMENT OF THE LANCELET

The egg is about 0.1 mm. in diameter, and has a thin vitelline membrane. Before it is laid, the egg undergoes the first maturation division, in which half the nuclear material and a very small amount of cytoplasm are separated as the first polar body. The second maturation division, with the formation of the second polar body, occurs just after fertilisation (Fig. 28.5). The ovum

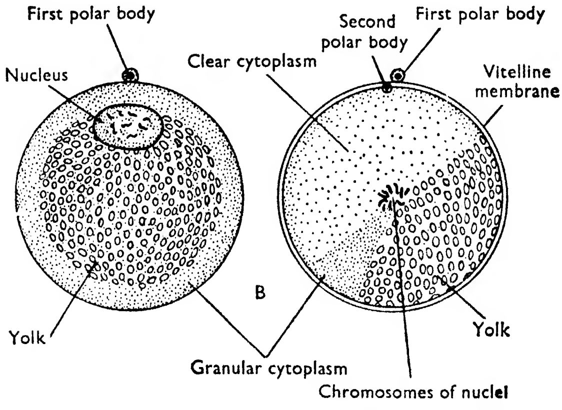


FIG. 28.5.—Ova of *Branchiostoma*. *A*, unfertilised ; *B*, after fertilisation.

is determinate, although the portions of the cytoplasm which are destined to form particular regions of the future body are not yet in position. Under the vitelline membrane is a layer of cytoplasm which is finely granular but free from yolk granules. Within this the cytoplasm contains yolk granules. A large nucleus (germinal vesicle) displaces it from a good deal of one side of the ovum ; this is the cytoplasmic pole. The cytoplasmic pole is usually spoken of as the upper side, but actually when the embryo is formed this side will be ventral and at the front end, while the yolky side will be dorsal and behind. On fertilisation the nuclear membrane of the germinal vesicle breaks down and a quantity of clear cytoplasm takes the place of the vesicle ; shortly afterwards the mingling of the two sets of chromosomes takes place near the middle of the egg. Meanwhile the granular cytoplasm which has covered the ovum flows to the vegetative pole and there becomes a crescent around the future posterior end. The clear cytoplasm which now forms the pole of the egg will give rise to the ectoderm, the yolky cytoplasm will give rise to the endoderm, and the crescent of granular cytoplasm between the two at the hind end will give the mesoderm. The first cleavage (Fig. 28.6) is vertical and forms two equal cells. The second is also vertical, at right angles to the first, but not quite equal, the third nearly equatorial, dividing each blastomere into a rather smaller upper half and a rather larger lower half. The cells do not meet in the middle, so that at this stage they form a ring. Division continues, and up to the 256 cell stage, which is reached at four hours, it is synchronous, that is, all the cells divide together. Eventually there arises a slightly pear-shaped blastula. Its wall consists of a single layer of cells, which differ somewhat in different regions. The ventral and anterior part is composed of small cells derived

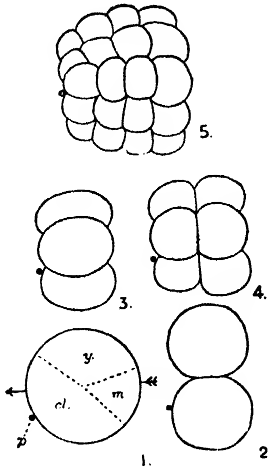


FIG. 28.6.—Early stages of the cleavage of the ovum of *Branchiostoma*.

1., Fertilised ovum ; *cl.*, clear cytoplasm which after cleavage will be situated in the ectoderm cells ; *m.*, granular cytoplasm which will be in the mesoderm cells ; *y.*, yolky cytoplasm which will be in the endoderm cells ; 2., first cleavage—stage of two blastomeres ; 3., four blastomeres ; 4., eight blastomeres ; 5., thirty-two blastomeres.

The figures are so posed that the side which will, in the adult, be dorsal is above, and that which will be anterior is to the left ; the horizontal axis of the adult is indicated by the arrow in No. 1. The animal pole of the ovum, indicated by the (second) polar body, is anteroventral.

from the clear cytoplasm of the ovum, the dorsal cells are larger and more yolky; a crescent around the posterior end is made up of smaller cells with granular cytoplasm (Fig. 28.7, B and C).

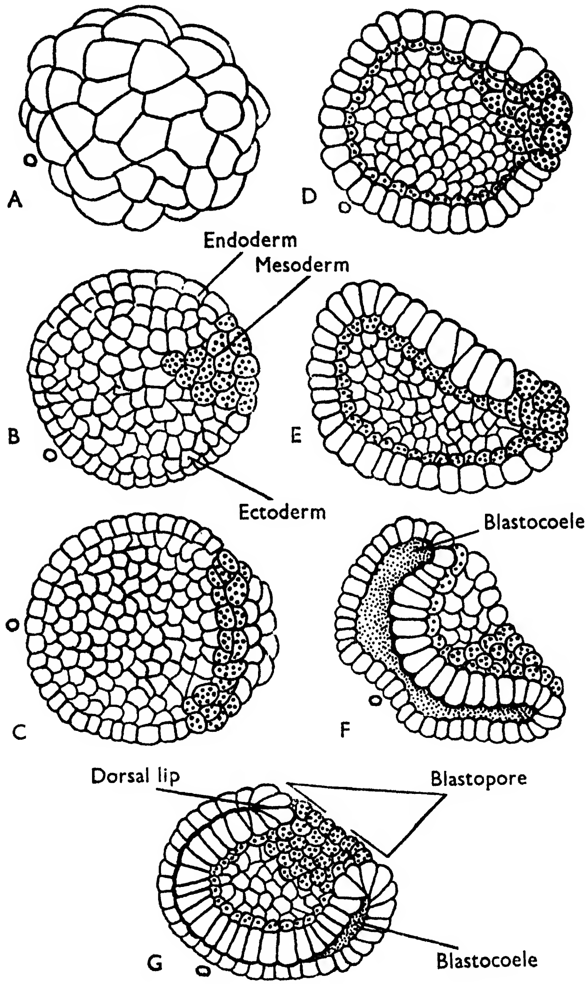


FIG. 28.7.—The gastrulation of *Branchiostoma*. *A*, 64-cell stage; *B*, completed blastula, from the side and slightly from the ventral surface, so that the mesoderm appears rather more dorsally than it really is; *C*, the same stage as *B*, from the ventral surface and slightly from behind; *D*, the same stage cut sagittally in half and viewed from within; *E*, an early gastrula, cut sagittally and viewed from within; *F*, and *G*, similar halves of successively later stages. The small circle in each drawing marks the position of the polar body.—Modified from Conklin.

GASTRULATION

Gastrulation (Fig. 28.7) begins by a flattening of the dorsal area of yolky cells. Next these are dimpled or invaginated into the blastocœle, forming a cup. The yolky cells—the endoderm or hypoblast—form the lining, while the blastopore, which is as yet very wide, has a lip composed above of small cells of the anteroventral area, now the ectoderm or epiblast, and at the sides and below of the cells of the crescent. The process continues by a rolling in over these lips, so that above ectoderm cells and at the sides the cells of the crescent become part of the lining of the cup. Meanwhile the embryo is lengthening, and the blastopore

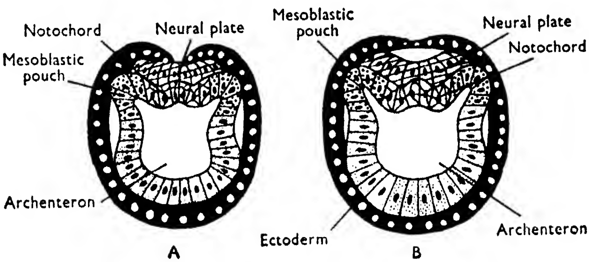


FIG. 28.8.—Diagrammatic transverse sections of embryos of *Branchiostoma* at the same stages as Fig. 28.9 *A* and *B*.—After Hatschek.

narrowing owing to the growth backwards of its anterior lip which, since it thus comes to cover the dorsal side, is known as the dorsal lip. The gastrula when it has thus been completed (Fig. 28.9) is elongate, with a small blastopore at the hind end of its flat upper side. Its cavity is lined below and at the sides by endoderm and has for its ceiling in the middle a strip of cells which rolled in over the dorsal lip and will form the notochord, and on either side of this a groove formed from the crescent cells. These cells are the mesoblast or the rudiment of the mesoderm. The cavity of the gastrula is the archenteron ; the blastocœle has been obliterated during the invagination.

Meanwhile the cells of the ectoderm develop cilia, by means of which the gastrula revolves within the vitelline membrane, and the cells of the flat dorsal side become more columnar and form a distinct strip known as the neural or medullary plate. The ectoderm at the sides of this plate now becomes detached from it and grows over it, enclosing a small space (Fig. 28.8).

This process begins at the hind end, so that the blastopore is covered and opens into the space in question (Fig. 28.9). The sides of the neural plate then fold upwards and meet above the space, so as to form a tube which will become the nerve cord. Its hollow is the neural canal, and the blastopore, which is now known as the neurenteric canal, leads from it to the gut. Eventually the neurenteric canal closes. An opening, known as the neuropore, long remains at the front end of the neural canal

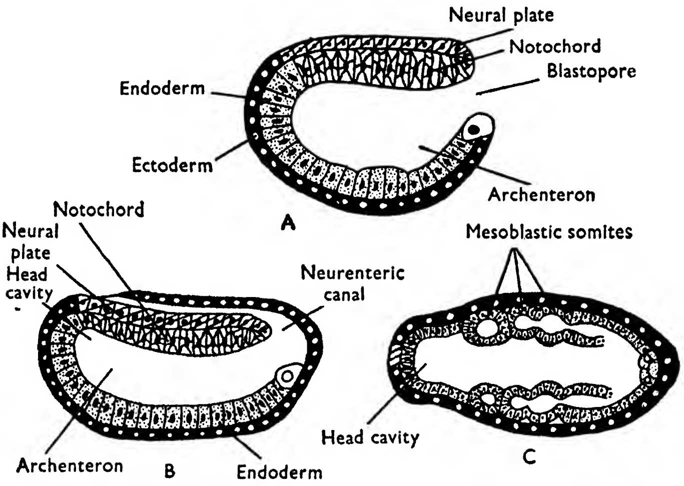


FIG. 28.9.—Diagrammatic longitudinal sections of embryos of *Branchiostoma*. *A*, sagittal section of completed gastrula; *B*, sagittal section of early post-gastrula; *C*, frontal section of same stage showing one completed mesoblastic somite.

and puts it into communication with the animal's olfactory pit (p. 306).

While these things are happening the ceiling of the archenteron gives rise to the notochord and to the mesoderm. The notochord is formed by a median longitudinal strip (Fig. 28.10) which becomes grooved and separated from before backwards, its cells eventually rearranging themselves to form a rod and becoming vacuolated. Its front end grows forwards to the end of the snout. The hind end is for a long time connected with the endoderm in front of the neurenteric canal. The mesoderm arises as hollow outgrowths (Figs. 28.8, 28.9, 28.10). One of these is median and unpaired in front. Behind it lies a pair of dorsolateral grooves at the sides of the notochord. The median pouch

soon separates from the gut, but the grooves, as fast as they close off in front, are prolonged backwards. As growth progresses the separated anterior part of the groove becomes segmented into a series of pouches. These pouches are the mesoderm segments or mesoblastic somites. They will presently spread between ectoderm and endoderm and give rise to the mesoderm of the adult. When the notochord and mesoderm have separated, the dorsal edges of the endoderm close in under them to form a complete tube, the enteron, which will become the alimentary canal of

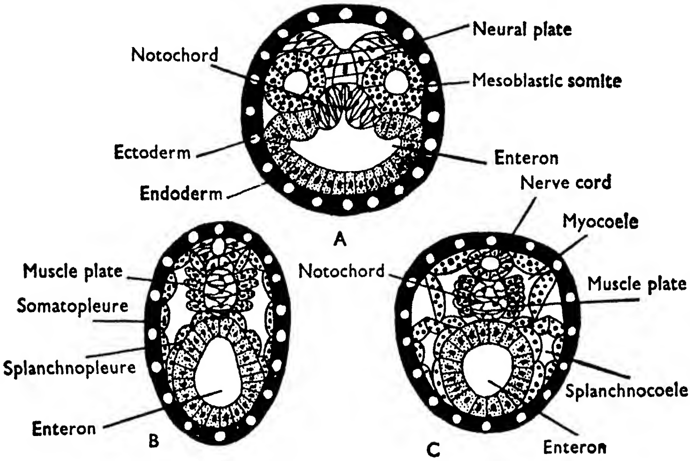


FIG. 28.10.—Diagrammatic transverse sections of embryos of *Branchiostoma* at stages successively later than those of Fig. 28.8.—After Hatschek.

the adult. The rudiments of all three layers of a triploblastic animal are now present.

LARVA

About eight hours after fertilisation and before the changes just described are complete, hatching takes place by the throwing off of the vitelline membrane. Until the formation of the mouth the animal is sometimes called the ‘ free embryo ’. About twenty-four hours later the mouth is formed as a small opening, which rapidly enlarges, on the left side of the forepart of the body. At the same time, by perforation from within outwards, the first gill slit is formed as a median ventral opening which shifts upwards to the right side of the body. As we shall see, this

slit belongs to the left side of the body of the adult. The anus is formed shortly after the first gill slit, much nearer the hind end of the body than it is in the adult. Development henceforward takes place more slowly, the animal becoming adult in about three months. We will consider first the external features of its metamorphosis. More gill slits are formed in the midventral line, and each in turn shifts on to the right side. They are primary slits, and each except the first acquires a tongue-bar. When fourteen of these slits have been formed, another series appears above them on the right-hand side. These are eight in number. Six of the first series of slits disappear, so that the number in the two series is the same. While the formation of the second series

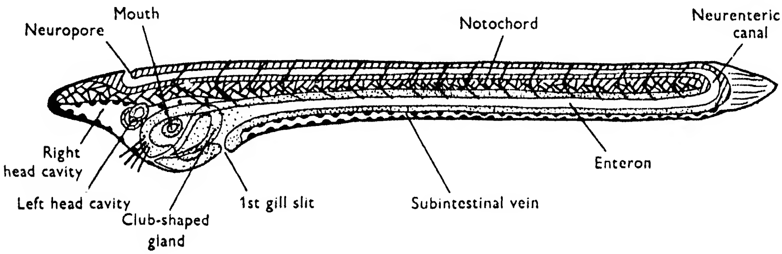
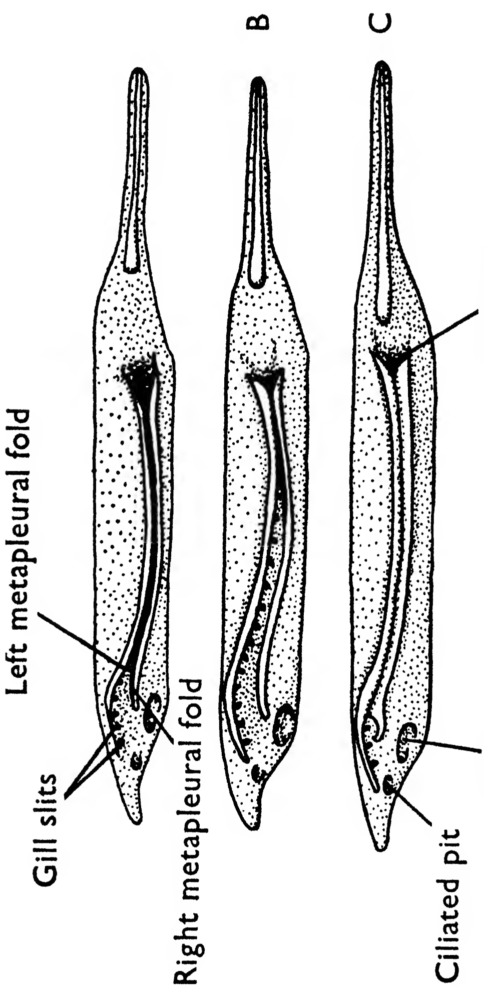


FIG. 28.11.—A diagram, partly in sagittal section, of a larva of *Branchiostoma* with one gill slit.—After Hatschek.

of slits is taking place both series shift downwards, the original series passing over to the left side of the body, while the second series remains on the right. At the same time the mouth also shifts to its adult position in the middle line. The slits at first open directly upon the surface of the body, but at an early stage, when there are as yet only six clefts of the first series, two longitudinal ridges appear, one on each side of the slits. In correspondence with the position of the slits these ridges lie in front on the right side of the body, but behind curve down to the ventral side, where the new slits are forming. These ridges are the metapleural folds. From the inner face of each a secondary ridge grows inwards to meet its fellow and enclose a space below the body. This is the rudiment of the atrium. As the ridges do not meet behind, there is left an opening which becomes the atriopore. The closure of the atrium takes place from behind forwards as the folds shift downwards with the clefts, from the right side of the body to their permanent position (Fig. 28.12). The atrium is at

first small, but enlarges so as to enclose the sides of the pharynx. The endostyle appears at the beginning of the larval period as a band of columnar ciliated cells on the right side of the anterior end of



G. 28.12. Three larval stages of *Branchiostoma*. metapleural folds are still separate; *B*, they are untied behind; *C*, they are united their whole length.—After Lankester and Wi ey.

the pharynx above the first gill cleft. It becomes folded as a V with the apex directed backward. When the two rows of clefts are established, the apex of this V grows back between them, the two limbs fusing to form a single strip. As the clefts move downwards the endostyle between them moves also.

MESOBLASTIC SOMITES

We must now consider the fate of the mesoderm rudiments. The median outgrowth divides into right and left halves, of which the right becomes a cœlomic cavity in the snout of the adult, while the left opens to the exterior and becomes Hatschek's pit in the wheel organ. Each of the somites of the first pair sends forward into the snout an outgrowth, which gives rise to a cavity in the head of the adult, while its walls form part of the mesoderm of the same region. The rest of the somite gives rise to other spaces in the neighbourhood of the mouth and by backward outgrowths to spaces in the metapleural folds. The walls of the spaces give rise to mesodermal tissues around the mouth and in the metapleural folds, and to the first myomere. The remaining mesoblastic somites all behave alike. They extend downwards on each side (Fig. 28.10) till they meet below the gut. The outer or somatic wall of each is called somatopleure, and the inner or splanchnic wall splanchnopleure, but these terms are sometimes taken to include the ectoderm or endoderm with which the layers are respectively in contact. The longitudinal septum or ventral mesentery between the cavities of the two sides now breaks down, so that they become continuous. The cœlom is thus formed by the coalescence of the cavities of pouches which have grown out from the archenteron, and is called an enterocœle. Meanwhile there has formed in each of them a horizontal septum which divides it into a dorsal half or epimere and a ventral half, the hypomere or splanchnotome. The cavity of the ventral portion is known as the splanchnocœle. The septa between the splanchnocœles break down so that they form a continuous perivisceral cœlom. The cavities of the dorsal parts of the somites remain separate and are known as myocœles. Their inner walls, against the notochord, become greatly thickened, each to form a structure, known as a muscle plate, which gives rise to a myomere in the adult, the walls between myocœles giving rise to connective-tissue septa between the myomeres, and the outer walls of the myocœles to the dermis. From the inner wall of each epimere, below the muscle plate, an outgrowth burrows its way between the muscle plate and the notochord and forms from its wall the connective-tissue sheath of the notochord and nerve cord. This outgrowth is known as the sclerotome, the main part, which contains the muscle plate, being known as the myotome. Lastly, in the pharyngeal region

the myotome grows down in the body-wall, between the splanchnocœle and the ectoderm, and at its lower end forms an outgrowth, the gonotome, which forms a gonad.

HABITS OF THE LARVA

During the external and internal changes which we have traced, the larval amphioxus swims freely in the sea, usually at a depth of a few fathoms from the surface. As its metamorphosis reaches completion, it sinks to the bottom and takes up the burrowing habits of the adult lancelet (see p. 298).

DEVELOPMENT OF THE FROG

The maturation divisions are similar to those of *Branchiostoma*. The cytoplasmic pole, while the egg is still in the ovary, has pigment granules in the cortex of the cytoplasm, just below the surface, while the yolky pole is packed with yolk granules and is unpigmented. The egg is enclosed in a vitelline membrane, and outside this there is added, as the egg passes down the oviduct, a layer of albumen which is probably bounded by another membrane. Pairing and fertilisation take place in water (p. 378). Many sperms appear in the albumen and make their way to the egg surface, but usually only one penetrates the vitelline membrane and enters the cytoplasm of the egg. A change in the vitelline membrane begins at this point and spreads in all directions so that it is transformed into the fertilisation membrane and is lifted up from the surface of the egg. The egg now rotates under the influence of gravity, so that the denser yolky pole lies below and the pigmented cytoplasmic pole uppermost. The path of the sperm nucleus to the egg nucleus usually lies above the equator, and directly opposite to the point of entry of the sperm (longitude 180°), pigment granules begin to drop in towards the centre of the egg. Yolky material moves towards the cytoplasmic pole to compensate for this, and in this region the pigment is observed through a yolky cytoplasmic film (Fig. 28.13). The falling-in of cortical material extends both ways round the egg at about the level of the Tropic of Capricorn (23.5° S) so that there is formed a just visible grey crescent.

Cleavage now begins. The first division passes through the poles and bisects the grey crescent, the second is at right angles

to this and also through the poles, while the third lies above the equator, almost at the Tropic of Cancer. The cleavage is therefore radial, and proceeds around the forming blastocœle until some 64 or 128 cells are present. The grey crescent has remained visible and undisturbed throughout, but is now distributed through several cells, and along it tissue begins to bulge into the blastocœle as a fold, resulting in what looks like a smile on the face of the egg. This is the beginning of the morphogenetic movements which constitute gastrulation.

The fate maps in Fig. 28.14 illustrate the following description.

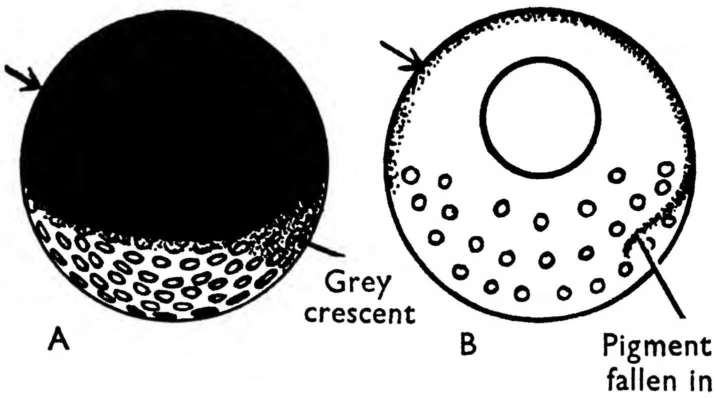


Fig. 28.13.—Fertilisation in the frog. The arrow shows the point of entry of the sperm. *A*, the whole egg, without its membranes ; *B*, sagittal section.

The tissue that bulges into the blastocœle also moves towards the cytoplasmic pole, but does not tear. A useful analogy is the deformation of a flaccid balloon by a hand pushed into it almost tangential to the surface. If this experiment is performed it will be seen that the corners of the groove (the original smile) must extend along their line of latitude in order that more tissue may be involved in the movement. In fact, in the frog's egg, the smile extends until its ends meet on the far side of the egg. During its progress tissue is rolling over its lips and becoming changed into primitive gut, notochord and mesoderm as it goes. That part of the lip which is first formed (in the original position of the grey crescent) has passing over it tissue which is transformed into notochord, and this lip will finally represent the most posterior end of the dorsal side of the embryo ; it is called the dorsal lip. The tissue rolling over the more lateral lips, and later over the

ventral lip when a full circle is complete, immediately splits into two layers. The inner layer, still in contact with the outside world,

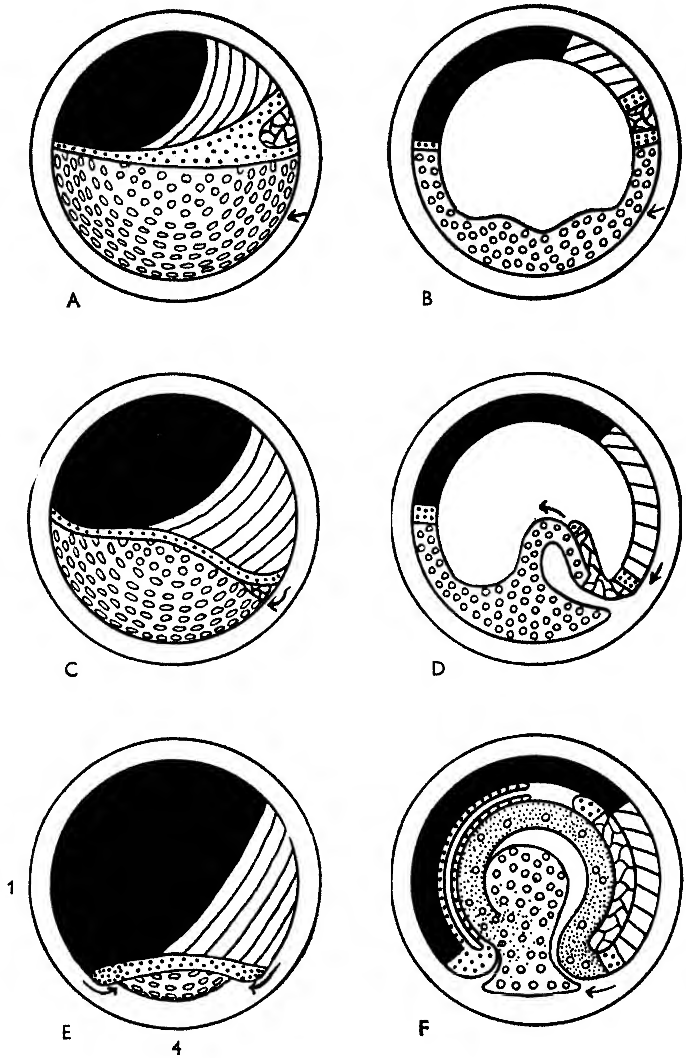


FIG. 28.14.—Diagrams of gastrulation in the frog. *A*, *C*, *E*, views of the whole embryo from the side, with presumptive areas marked; *B*, *D*, *F*, corresponding sagittal sections. Arrows show the direction of movement of cells, and the numbers in *E* the position of the sections of Fig. 28.15 *C* and *D*.

will be the wall of the gut, while the other, lying between the gut and that tissue which does not roll in, will form the mesoderm.

This mesoderm itself splits into two layers ; one, apposed to the gut, is splanchnic, the other, against the inner aspect of the surface

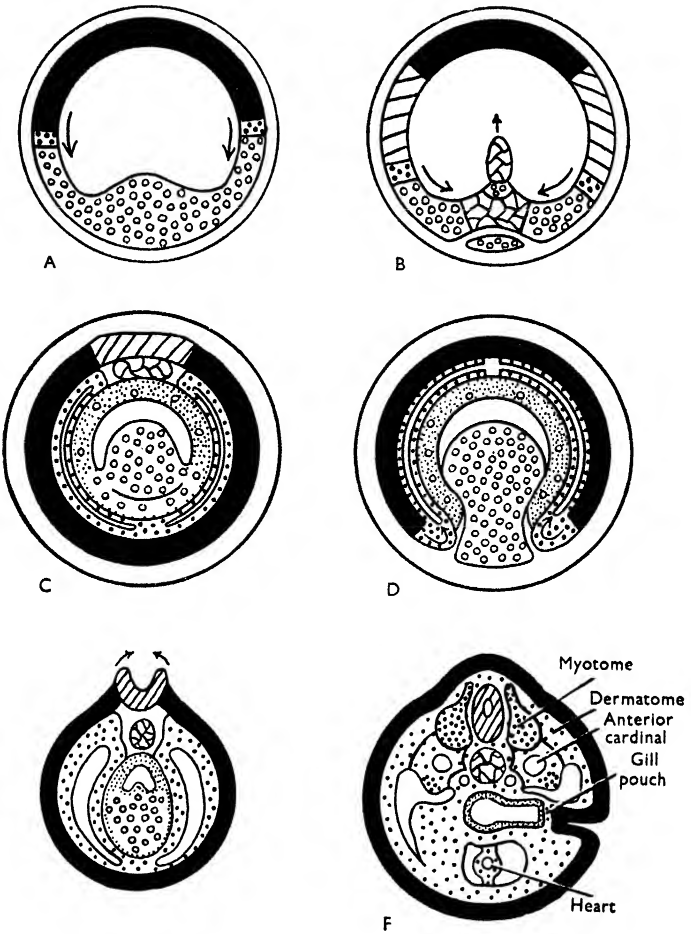


FIG. 28.15.—Diagrammatic sections of frog embryos. *A*, transverse section of stage of Fig. 28.14 *A* ; *B*, transverse section of stage of Fig. 28.14 *C* ; *C*, transverse section of stage of Fig. 28.14 *E*, through 1 and 2 ; *D*, frontal section of stage of Fig. 28.14 *E*, through 3 and 4 ; *E*, transverse section of trunk of early neurula, stage of Fig. 28.16 *A* and *B* ; transverse section through late neurula at the level of the heart, stage of Fig. 28.16 *C*.

tissue, is somatic. The space which appears between them will become the cœlom (Figs. 28.15 and 28.16).

The embryo is now a gastrula, with the primitive gut or archenteron extending until it almost reaches its anterior wall. Mean-

while the yolky cells have passed over or have been engulfed by the lateral and ventral lips which mark the open edge of the archenteron, or blastopore. Once this has become a complete ring by the formation of the ventral lip it can only decrease in circumference as more tissue rolls over to the inside, until finally it

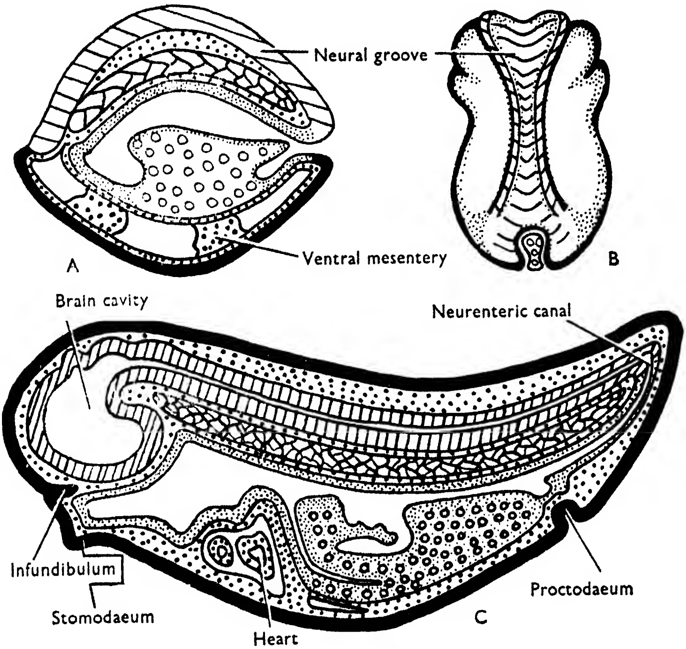


FIG. 28.16.—Diagrams of the neurula of the frog. *A*, a sagittal section with open neural groove; *B*, dorsal view of same stage as *A*, showing the blastopore; *C*, sagittal section at hatching; cf. Figs. 28.4 and 28.17.

shrinks to a small circle that bounds a mass of yolk that has not been completely engulfed, the yolk plug (Fig. 28.15 D).

As the tissue that rolls over the dorsal lip changes into notochord it has an organising action on the tissue lying immediately above it, so that this overlying tissue, called the neural plate, will form the dorsal nerve cord. This stage is the neurula. Around the area of the notochord and neural plate, tissue tends to move towards the midline of the animal, so that the more dorsal region of the gut becomes long and narrow, as does the notochord, which now becomes completely separated from the underlying gut. The neural plate forms two parallel ridges which then arch over the groove that appears between them (Figs. 28.15 and 28.16); in

this way a hollow longitudinal tube is produced. It separates completely from the tissue adjacent to it, which then heals over in the dorsal midline. At the anterior end the lumen of the tube is open to the outside world through a small hole, the neuropore, while at the posterior end the neural folds extend on either side of the blastopore, recruiting material from the lateral lips, and then arch over and fuse. The archenteron thus has a connection with the lumen of the neural tube through a small neurenteric canal (which has been known to persist into adult life in man) but the blastopore loses its connection with the outside world except through the length of the tube and the neuropore.

The strip of cells on each side of the neural plate, furthest from the inductive influence of the notochord, does not take part in the formation of the neural tube, but appears as a ridge on its dorsolateral surface, where it is known as the neural crest. It soon breaks up, and its cells drop into the underlying mesoblast, and later give rise to many important parts of the body.

ALIMENTARY SYSTEM

When the neural canal is fully formed the gut or archenteron is a tube, composed wholly of hypoblast, stretching from nearly the anterior end of the embryo to the neurenteric canal (Fig. 28.16 C). Just in front of the extreme anterior end, and slightly ventral to it, the ectoderm thickens and begins to dimple inwards. This dimple is the stomodæum, and as it grows it breaks through and joins the archenteron. A similar ectodermal invagination just ventral to the old position of the blastopore forms the proctodæum, which also opens into the archenteron. The gut now has the formal outlines of the adult structure : an anterior opening, the mouth, leading to an ectodermal foregut ; a midgut or mesenteron of endoderm ; and an ectodermal hindgut, opening to the exterior by the anus, which is not at the posterior end of the body.

Before this arrangement is complete other changes have taken place in the midgut. In its anterior part or pharynx four bulges start outwards on each side, and meet corresponding inpushings of ectoderm ; the result is four pairs of lateral channels, the gill pouches, with openings to the exterior, the gill slits (Fig. 28.15 F). Other diverticula from the midgut form lungs, liver and pancreas, some details of which will be found in Chapter 27.

MESOBLAST AND NERVOUS SYSTEM

The mesoderm of the frog is not typical of vertebrates, since even in the dorsal region it is not fully segmented. The mesoblast of the trunk forms a number of segmental blocks, the epimeres, which develop from before backwards, and become the skeletal muscles. Most of the other mesodermal tissues, including the skeleton, blood vessels, visceral muscles, and all the muscles of the head, arise from a loose tissue called mesenchyme, which is so liquid in the head that it is sometimes described as 'mesodermal porridge'. Though mainly derived from mesoblast it contains also cells derived from both hypoblast and epiblast, and especially from the neural crest.

The nerves and nervous system develop in the manner normal for vertebrates, but as their arrangement is seen best in animals where the mesoblast is more fully segmented, a description of them is postponed until we come to the chick (p. 665).

CŒLOM AND VASCULAR SYSTEM

At about a third of the way from the front end the splanchnopleure and somatopleure come into contact again and fuse, so that the cœlom is not continuous from end to end but is divided into anterior and posterior cavities. It gradually expands, especially in the posterior portion, so that the gut comes to be slung from its roof and anchored to its floor by the dorsal and ventral mesenteries respectively (Figs. 28.15 E and 28.16 A). The posterior cavity, containing most of the gut, is the peritoneal cavity, and its somatic wall the peritoneum. The anterior wall of the peritoneal cavity, where splanchnopleure and somatopleure meet, is the transverse septum, and in the ventral mesentery in front of this the heart is formed, the portion of cœlom surrounding it being the pericardium. Meanwhile other parts of the vascular system are being formed elsewhere in the mesoblast, which breaks down to form a fluid surrounded by mesoblastic walls and containing cells, also derived from the mesoblast, which are the blood corpuscles. This liquefaction occurs in several places at once, which gradually become connected to form the main blood sinuses. Blood finally flows down around the gut in the splanchnopleure,

and it is the dilatation of these vessels which expands the splanchnic layer to meet the somatic layer and form the transverse septum. This blood enters the heart posteriorly, although the heart may have formed muscle fibres and begun to beat before this happens. Blood is forced forward out of the heart, goes through the branchial arches to the dorsal aorta, and the main lines of the circulation are established.

LARVA

About a fortnight after the eggs are laid and shortly before the mouth and anus break through, the embryo leaves the jelly in which it is embedded and becomes free-living. Since it possesses

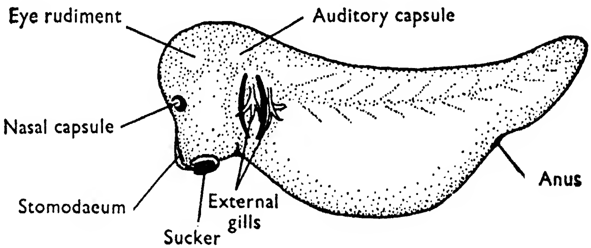


FIG. 28.17.—A newly-hatched embryo of a frog.

features not present in the adult it is, in the strict sense, a larva. Amongst these are a number of external features, which, on account of the ease with which they can be observed with a hand-lens, have obtained a disproportionate importance in examination syllabuses. At hatching the larva has the appearance shown in Fig. 28.17. Below the beginning of the stomodæum is a crescent-shaped sucker, by which the animal can attach itself to pondweeds; and above the ridges of the first two branchial arches, that is, between the first and second and second and third gill slits, are branched external gills. Soon afterwards a third pair of these appears behind the first two and when the stomodæum breaks through to the gut there forms above and below the mouth a pair of horny jaws.

Meanwhile four gill slits open, and the external gills wither, being replaced by new gills on the walls of the slits. The latter

represent the first to fourth branchial slits of the dogfish, the external gills standing on the first three branchial arches. Shortly after the appearance of the slits a fold of skin grows back from each side of the head so as to cover them. The folds are the opercula ; they meet ventrally, and presently their hinder edges fuse with the body everywhere, except in one spot on the left side, where an opening is left for the discharge of the water used in breathing. The sucker now begins to degenerate. Shortly afterwards, rudiments of the hind-limbs appear at the base of the tail, as a pair of small knobs, which increase rapidly and become first jointed and then divided into toes. The fore-limbs arise at the same time as the hind-limbs, but as they are covered by the opercula they are not seen till a later stage. About the end of the second month the lungs which have been forming come into use and the gills start to degenerate, and a fortnight later the tadpole begins to turn into a young frog. The outer layer of the skin and the horny jaws are thrown off, the mouth enlarges and changes its shape, the fore-limbs appear, that on the left being pushed through the gill opening, that on the right breaking through the operculum, the gill slits close, and finally the tail shortens and is absorbed, and the metamorphosis is complete. All these changes take place through the influence of the hormone of the thyroid gland.

DEVELOPMENT OF THE GUPPY

The egg of a teleost fish consists of a large mass of yolk with a relatively small patch of cytoplasm, the blastodisc, sitting on top of it. The guppy (*Lebistes reticulatus*), which is easily kept and studied in the laboratory, is one of the few teleosts in which fertilisation is internal, and the eggs are hatched inside the body, so that the animal is said to be ovoviviparous. The anal fin of the male is rolled to form the gonopodium, which injects the sperms into the female. They may be stored for a considerable time in her genital tract, and one mating may be enough for ten batches of young. The sperms penetrate the vitelline membrane from the inner aspect of the hollow ovary, and one of them unites with the egg nucleus, which lies in the blastodisc ; many other sperm nuclei are present round the blastodisc and form asters, so that there is polyspermy. The first six or seven divisions are vertical and extend only to the blastodisc ; only then is there a chordal (or horizontal)

division. Successive cleavages, vertical, horizontal and irregular, result in an embryo comparable with the blastula of the frog, but whose blastocœle is only nominal ; it is called a blastoderm, and lies on top of the yolk.

The gastrulation movements are at first sight very different from those of the frog. Tissue at one end of the blastoderm rolls under and into its mass to form the notochord, so that it may be equated to the dorsal lip of the blastopore. The rest

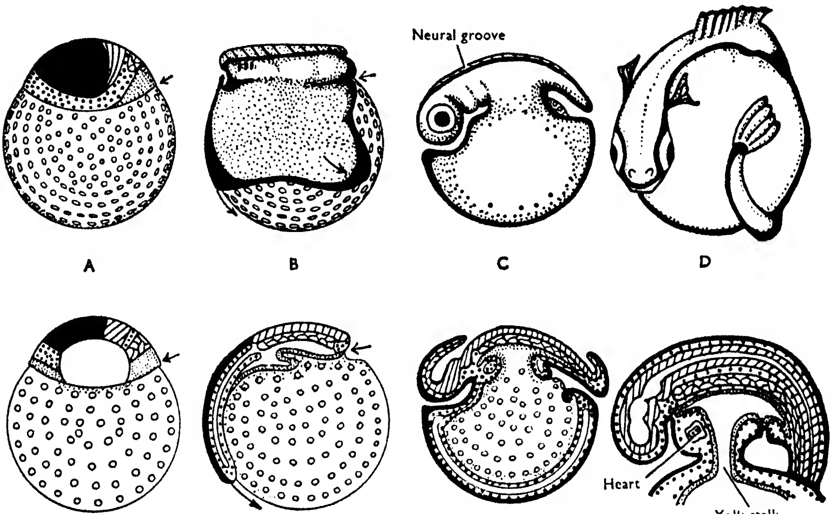


FIG. 28.18.—The development of the guppy. Upper row, the whole embryo with the membranes removed ; lower row, diagrammatic sagittal sections of the same stages.

of the circumference of the blastoderm extends outwards over the surface of the yolk (Fig. 28.18 B) and possibly tissue rolls over its edge all round. If this happens, these edges of the blastoderm are comparable with the lateral and ventral lips of the frog's blastopore, and the covering of the yolk is comparable with the contraction of the blastopore to enclose the yolk-containing cells of the frog. As there is more yolk in the fishes its engulfment takes much longer than does that of the frog, and the embryo is usually fully formed as a result of the movement round the dorsal lip before the yolk is completely covered. We therefore have a real little fish lying on top of a ball of yolk, with a blastopore which is still open (Fig. 28.18 D).

DEVELOPMENT OF THE CHICK

The egg of a bird, for instance that of the common fowl (Fig. 28.19) consists of a large yellow yolk with a small circular blastodisc on top of it. There is a vitelline membrane and in this state the egg leaves the ovary. High in the oviduct it meets the sperms that have been injected in copulation, and although many usually penetrate the vitelline membrane only one completes the fertilisation. The vitelline membrane becomes the fertilisation membrane, and as the egg passes down the oviduct further layers are added : the white or albumen, which is a solution of proteins and salts ;

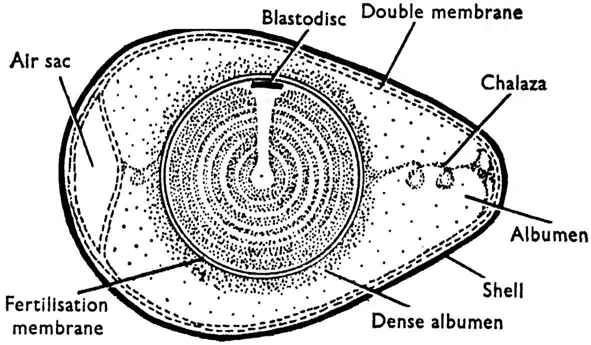


FIG. 28.19.—Diagrammatic sagittal section of a hen's egg.

then a double membrane whose two layers part at the broad end and so enclose an air space ; and finally a porous chalky shell. The white provides additional food, but its chief function is to supply water, without which the egg could not develop on dry land. Birds, indeed, have over-compensated for the dryness of their environment, and their eggs actually lose water during their development ; if the atmosphere is too damp for this to happen they die.

Cleavage begins while the egg is still in the oviduct with the formation of a furrow across the germinal disc but not reaching to its edge. This is soon crossed by another furrow, and then more appear until the disc is divided into a mosaic of irregular segments not fully separated from the underlying yolk (the ' subgerminal cavity ' seen in vertical sections is an artefact produced by the fixative. The segmentation is thus incomplete or mesoblastic (Figs. 28.20 and 28.21). Horizontal divisions occur, so that a

blastoderm two or three cells thick is formed; the top layer becomes regularly arranged and is the epiblast, while below it, separated by a very slight chink, the blastocœle, is a more irregular hypoblast. At this stage the egg is laid. It may survive

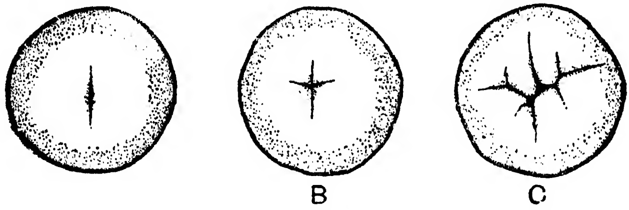


FIG. 28.20.—Views of the young blastoderm of the chick in three successive stages of cleavage.

for some days at atmospheric temperatures without development, but this begins again as soon as the mother begins to sit or the egg is put into an incubator. Many of the changes that occur

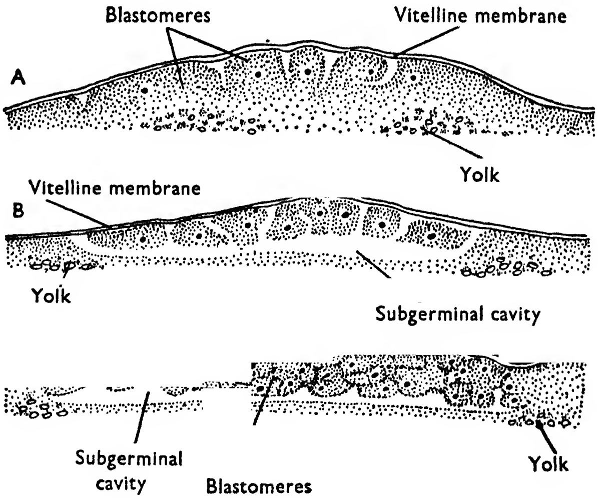


FIG. 28.21.—Slightly diagrammatic sections through the blastoderm of a chick. *A*, the stage of Fig. 28.20 *C*; *B*, and *C*, successively later stages.

can be seen if the egg is observed under a dissecting microscope through a window cut in the shell.

The blastoderm spreads over the yolk, chiefly because as the cells of the edge, called the germinal wall, divide, their nuclei incorporate some of the yolk around them. In a surface view of the

embryo there is now a translucent area pellucida, in which alone the body of the chick will be formed, surrounded by a whitish area opaca. In the centre of the epiblast there appears a wrinkle very similar to that produced on porridge by a nail dropped on it. This is the primitive streak, and marking points on the epiblast with vital stains shows that tissue is moving from either side towards it (Fig. 28.22 A). At the anterior end superficial tissue is moving backwards in the axis of the future embryo and then

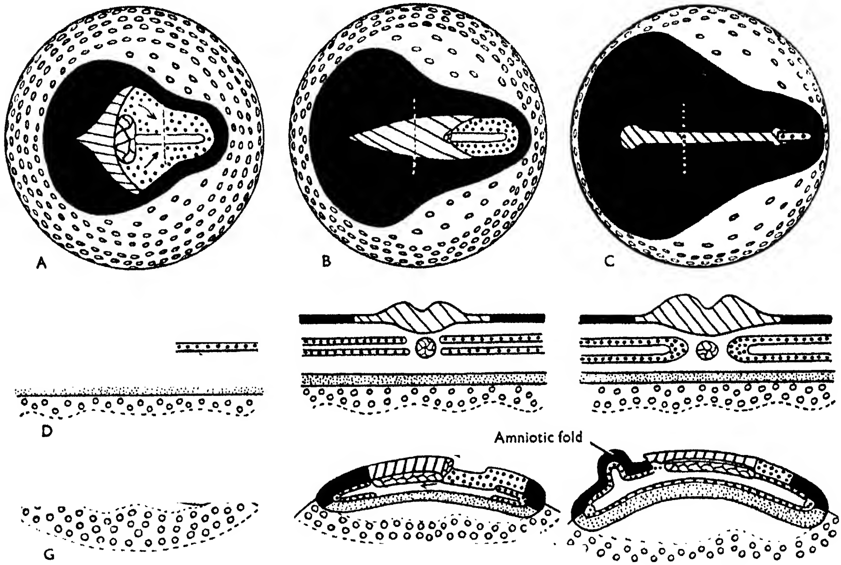


FIG. 28.22.—Diagrams of the development of the chick. Upper row, surface views of the blastoderm with the presumptive areas ; middle row, enlarged transverse sections in the planes of the dotted lines in the upper figures ; lower row, corresponding sagittal sections, slightly enlarged. Arrows show the direction of movement of the cells.

rolling over and passing under itself (arrows in Fig. 28.22 H). It comes to lie between hypoblast and epiblast and forms the notochord, anterior to the primitive streak. Along the length of the streak tissue is moving from further laterally, rolling over the lips of the streak, and passing into the space between hypoblast and epiblast, where it splits into splanchnic and somatic layers, with the cœlom between them (Fig. 28.22 D). They proceed anterolaterally, remaining in contact with hypoblast and epiblast respectively.

The tissue that is left above the notochord after these movements is transformed into a neural plate under the influence of

the organiser, as in the frog, and the plate bends up, drops into the tissues, and so becomes a neural tube. Meanwhile the hypoblast arches up in the mid-line much as does that of the frog, and forms the roof of the gut, but at this stage the gut has no floor. During all this the blastoderm has been extending, but the yolk is not completely covered until just before hatching, and

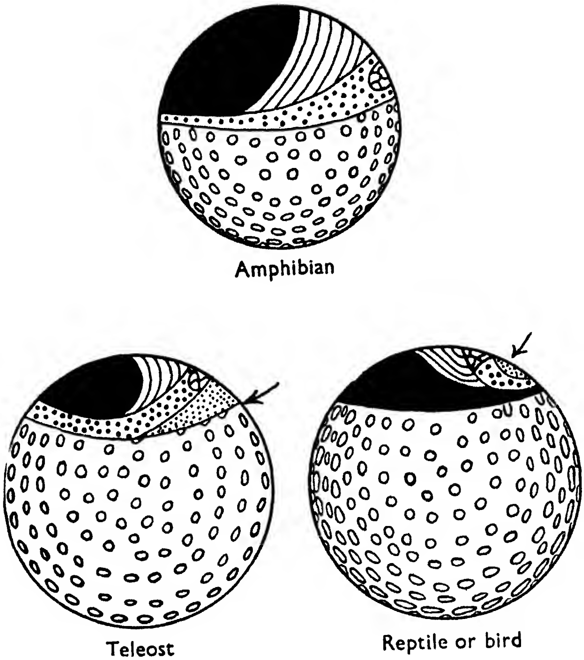


FIG. 28.23.—Vertebrate fate-maps. The arrow indicates the position of the blastopore.

even then a pore may remain (Fig. 28.24 C). The somatopleure which passes anteriorly by the sides of the notochord is organised into discrete lumps, the somites, which will form the embryonic musculature and much else ; their number is increased as more epiblast dives into the primitive streak and becomes mesoderm. The axial hypoblast, which is already arched, bulges forward under the head, producing a pocket of gut. The back edge of this pocket is called the anterior intestinal portal (from Latin *porta*, a gateway) (Fig. 28.24). Within the mesoderm lying in this fold the heart soon develops. Later, a similar pocket appears in

the hind region of the body, under the forming tail, and makes the posterior intestinal portal.

The region just anterior to the primitive streak (Hensen's node or the primitive knot) produces notochord, and so corresponds to the dorsal lip of the frog, while the primitive streak itself, where the more lateral mesoderm is formed by involution, is comparable to the lateral and ventral lips, but the blastopore is never open. If the fate maps of frog, fish and chick are compared it will be seen that the anteroposterior sequence of presumptive areas is similar in all three (Fig. 28.23). This situation may be stated in words as : the notochord is formed by tissue rolling over the dorsal lip (a little head mesoderm called prechordal plate rolls in before it), and this organises the tissue above it to become neural ; behind and at the sides of the notochord is tissue which will become mesoderm ; that tissue which has not been involved in these movements and is left on the outside becomes ectoderm.

EMBRYONIC MEMBRANES

The developing blastodisc of both fish and bird comes to surround the yolk completely, forming a membrane, the yolk sac. As the yolk is absorbed the sac shrinks towards the developing embryo, until it finally forms the floor of the midgut.

In the reptiles, birds, and mammals (the Amniota) other embryonic membranes are formed. After the chick has been incubated for about 36 hours the outer layers of the blastoderm begin to rise up as a fold in front of the embryo. This fold spreads laterally, and finally the two ends meet a similar fold that has started posteriorly. While this has been going on the fold has been rising up and arching over the embryo, and by 96 hours the margins of the fold have met and fused, so that only a small pore remains (Fig. 28.24 B). The result is that the embryo is covered by two membranes, the inner amnion and the outer chorion, each consisting of a sheet of ectoderm and a sheet of somatic mesoderm. The space between the amnion and chorion, which is lined by somatopleure, is part of the cœlom but is extra-embryonic ; the space between amnion and embryo, the amniotic cavity, is filled with fluid, and probably cushions the embryo against minor shocks, such as those caused when the parent bird turns the egg.

While the amnion has been forming, the hypoblast has been

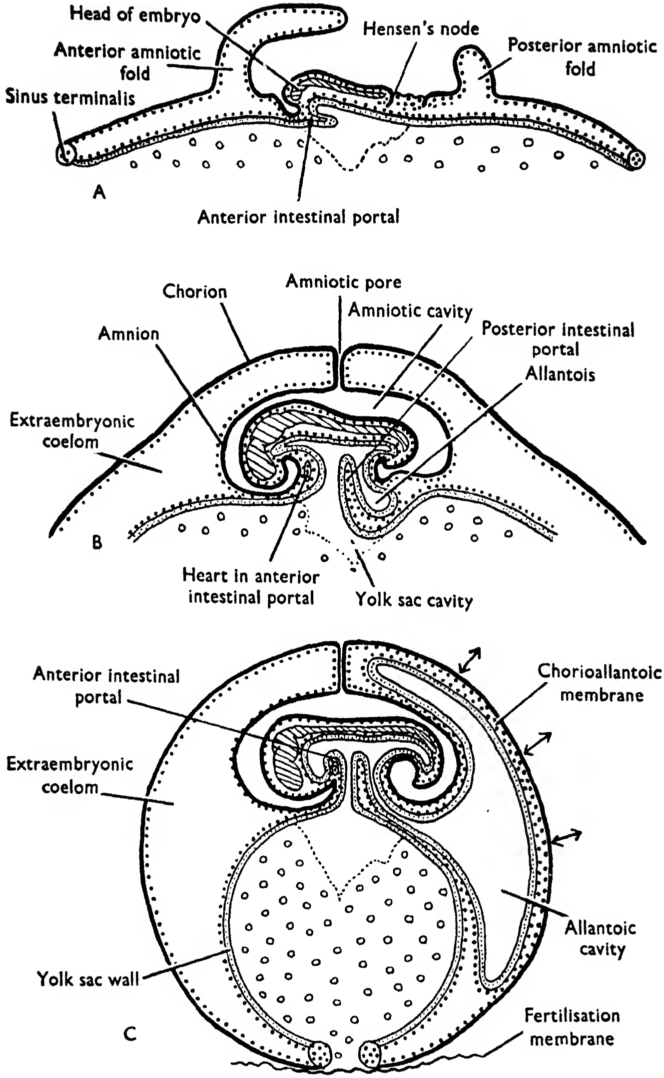


FIG. 28.24.—The embryonic membranes of the chick. Sagittal sections. *A*, about 48 hours, the anterior fold is well-developed and the posterior fold is beginning; *B*, about 96 hours, the amnion is almost complete and the allantois has begun; *C*, about 7 days, the allantois has expanded into the extraembryonic cœlom, and its splanchnopleure has fused with the chorionic somatopleure to form the chorioallantoic membrane; where the yolk is not completely enclosed, in the region of the sinus terminalis, the fertilisation membrane persists. The arrows indicate exchange of gases with the environment.

extending over the yolk in both the transverse and the longitudinal axes and the anterior and posterior intestinal portals have been approaching each other so that a floor is produced for most of the gut and the embryo is raised from the yolk sac, to which it is now connected only by a narrow stalk (Fig. 28.24 C).

After about 80 hours of incubation there grows out from the gut a ventral diverticulum, the allantois (Fig. 28.24 B). Its position shows that it is covered with splanchnopleure and projects into the cœlom below the gut. As it grows it falls over the posterior intestinal portal and spreads ventrally round the yolk sac into the extraembryonic cœlom, and dorsally into the cœlom between amnion and chorion (Fig. 28.24 C). Finally its outer layer, which is splanchnopleure, meets and fuses with the somatopleure of the chorion, so that a compound structure, called the chorioallantoic membrane, is formed, It becomes closely applied to the inside of the shell and highly vascular, and is the chief respiratory organ of the growing chick. The allantois has also an excretory function, crystals of uric acid being deposited in it and shed when it is cast off.

MESOBLAST AND NERVOUS SYSTEM

The paired mesoblastic somites, lying on each side of the neural tube, soon become divided, probably under the inductive influence of neural tissue medially, of skin laterally, and perhaps gut ventrally. Each forms four regions. Dorsally and near the notochord is a myotome ; this is the largest, and from it most of the muscles will arise. Outside it is a dermatome, which will contribute to the dermis of the skin. Below is a nephrotome, which will form the kidney, and a gonotome which will form the gonad. The last two are at first indistinguishable as the intermediate cell mass. The loose mesh of cells separating successive myotomes is the myocomma whose ventral portion becomes the sclerotome (cf. Fig. 27.17).

Before this has happened the neural tube has expanded greatly in the head region, to form the beginning of the brain. At the same time it becomes bent downwards, so that there is a cephalic or cranial flexure of nearly a right angle. The swelling that forms the brain is not uniform, but is clearly divided into three regions, the fore-, mid- and hind-brain.

Each myotome induces cells of contiguous neural tissue to grow out from the wall of the tube, and the group of processes so formed makes a ventral nerve root, which is thus segmental in origin and corresponds to the somite, to which in fact it runs. In animals such as the frog, where the mesoblast is not clearly segmented, the arrangement of the ventral roots is taken to represent the segmentation.

Above each myocomma, and so in an intersegmental position, cells of the neural crest aggregate to form a dorsal root ganglion. From this cells grow in two directions to form the dorsal nerve root : into the spinal cord as preganglionic fibres, and behind the myotome to form sensory cells on the surface of the body and elsewhere. Except in the head the dorsal and ventral roots join to form mixed nerves. A branch from the dorsal root carries cells down to form the sympathetic ganglia intersegmentally.

BLOOD VESSELS

The blood, its main vessels, and the transverse septum are formed much as they are in the frog. Much of the blood lies in two main drainage channels, the cardinal sinuses, lying one on each side dorsally. A vessel, the common cardinal, divides each

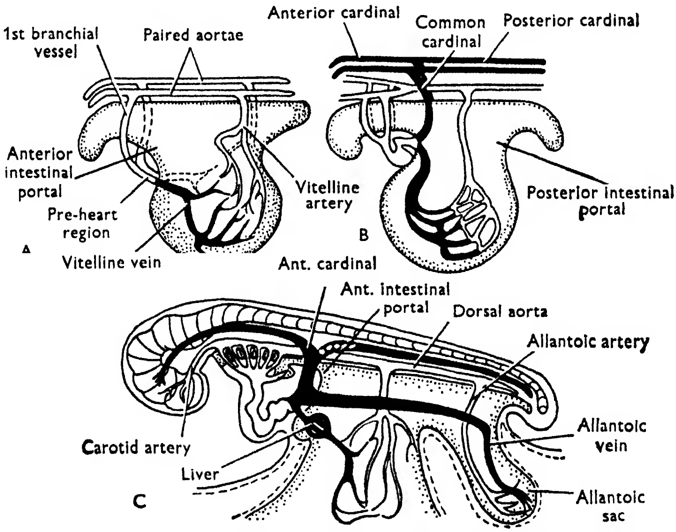


FIG. 28.25.—Diagrams of the development of the blood vessels in the chick. In *A* and *B* only the blood vessels, the gut and the yolk are shown ; in *C* the outlines of the skin and nervous system are shown, but only a portion of the yolk sac.—Based on Nelsen, *Comparative Embryology of the Vertebrates*, 1953, Blakiston, New York.

sinus into an anterior and a posterior portion, and runs down the transverse septum to unite with its fellow behind the heart to form the ductus Cuvieri. Meanwhile blood forced into the dorsal aorta through the branchial vessels has spread out over the yolk through several large vessels, the vitelline arteries, into a series of rivulets which at the boundary of the extending blastoderm

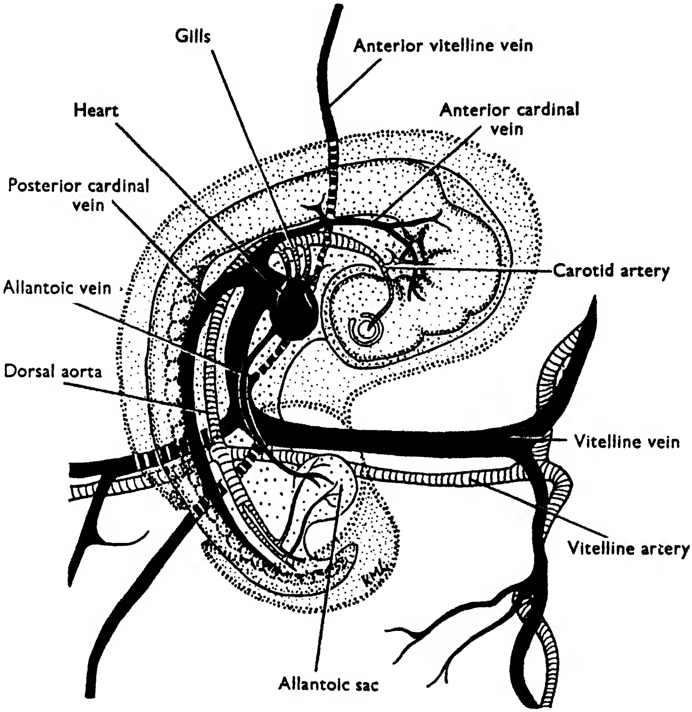


FIG. 28.26.—The blood vessels of the chick at about 80 hours' incubation.

form a ring-vessel, the sinus terminalis. (The blood in this clots and darkens if the chick dies and can then be seen through the shell.) From these vessels on the yolk sac, two major channels, the vitelline veins, converge upon the ductus Cuvieri and break into it (Fig. 28.25 B). There is some evidence that most of the blood corpuscles in the developing circulation come from the extraembryonic splanchnopleure of these vessels. The vitelline veins, which run round the anterior part of the gut when the anterior intestinal portal has moved backwards, are broken into by the liver; their posterior portion then becomes the hepatic

portal vein and the anterior part the hepatic vein. The kidneys similarly interrupt the flow of the posterior cardinal veins, whose posterior portions persist as small renal portals.

DEVELOPMENT OF THE RABBIT

The monotremes lay large yolky eggs, and their development is very similar to that of the chick. Other mammals have small ova with hardly any yolk, yet they produce membranes comparable with those associated with the yolk in birds (and reptiles) and their development is best understood by comparison with that of the chick.

The ovum of the rabbit, which is about 0.5 mm. in diameter, has no true vitelline membrane, but on discharge from the Graafian follicle it is surrounded by a thick membrane, the zona radiata, and by a layer of albumen, both secreted by the ovary, and by cells of this making the corona radiata. Sperms penetrate all three layers, the cells of the corona fall off, and fertilisation occurs in the upper part of the oviduct. Cleavage results in a solid pack of 8–16 cells, the morula (Fig. 28.27); division continues, and shortly afterwards, usually just before the embryo has reached the uterus, a cavity appears among the cells. Its subsequent history shows that it is not comparable to a blastocœle, so that the hollow ball of cells is called not a blastula but a blastocyst.

One or two of the cells of the morula may be already determined, and only a few of those of the blastocyst will take any part in the formation of the embryo, the rest giving rise to the extra-embryonic membranes and being later discarded. Those cells which will form the embryo divide rapidly in several planes, forming the inner cell mass, which projects into the cavity of the blastocyst. The other cells divide in a radial direction only, and at the same time they stretch, flatten and absorb water from the uterus, passing it on to the cavity, so that they form an expanded single layer, the trophoblast, and the blastocyst comes to resemble a bladder with a knob of cells projecting inwards at one point (Fig. 28.28 A). The subsequent history of the trophoblast shows that it is comparable to the ectodermal portion of the chorion of the chick. The cells of the trophoblast begin to invade the wall of the uterus, so that the embryo becomes firmly attached, and food materials diffuse from the maternal blood. At this time the

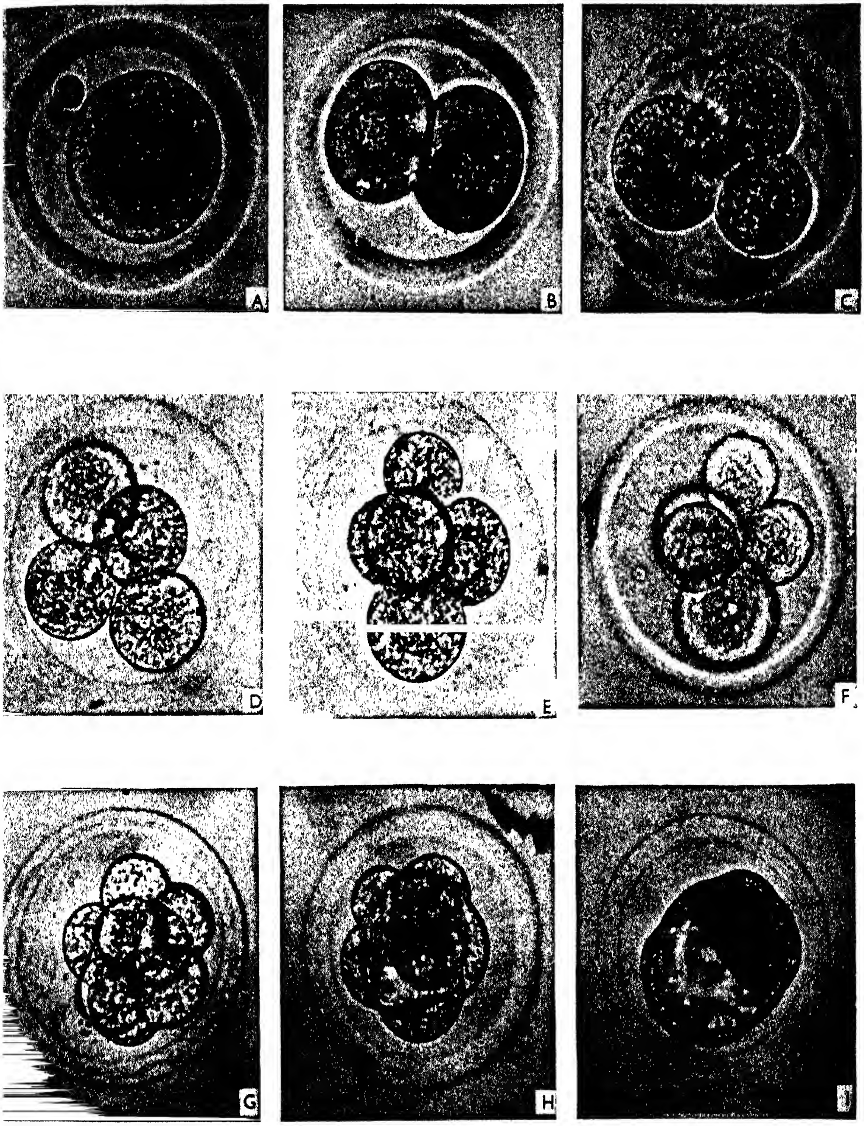


Fig. 28.27.—Fertilisation and cleavage stages of living eggs of the golden hamster. × 300.—From Boyd and Hamilton in Marshall's *Physiology of Reproduction*, 3rd edition, 1952. Longmans Green, London.

blastocyst is a long ovoid, with the inner cell mass midway along its length and against the uterus.

The cells of the trophoblast continue to flatten, and the inner-

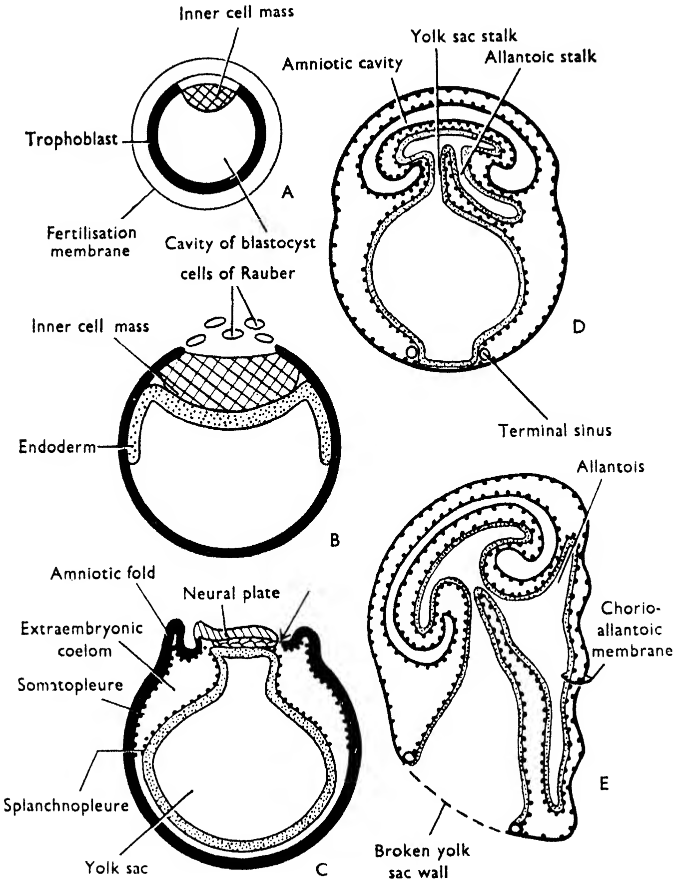


FIG. 28.28.—Diagrams of the early development of the rabbit, sagittal sections. *A*, early blastocyst ; *B*, the endoderm is forming and the cells of Rauber are beginning to break up ; *C*, the yolk sac is complete and mesoblast and amnion are forming ; *D*, the amnion is complete and the allantois has begun ; *E*, the chorioallantoic membrane has formed.

most layer of the inner cell mass becomes recognisably different from the rest. Its cells divide and migrate laterally on to the inner aspect of the trophoblast (Fig. 28.28 B). Since they will form the wall of the gut, the yolk sac and the allantois, they are hypoblast

Meanwhile, the trophoblastic cells above the inner cell mass, the cells of Rauber, break apart and are lost, exposing the outer surface of the inner cell mass, the embryonic disc, to the uterine cavity. On the surface of this disc a longitudinal primitive streak and primitive groove appear, and along their length cells drop in and spread outwards much as they do in the chick. They emerge as two layers of mesoblast, one, which is somatic, against the inner surface of the trophoblast, the other, which is splanchnic, against the outer surface of the hypoblast. At the anterior end of the streak there is a thickening, Hensen's node, and here the cells that sink in and pass forwards become, as in the chick, notochord, and induce the overlying cells of the disc to form a neural plate. The mesoblast never reaches the ventral pole of the blastocyst, so that hypoblast and trophoblast (which may be regarded as epiblast) are here in contact. These layers later break down, so that there is an opening from the uterine cavity into the gut of the embryo; through this route molecules of antibodies (p. 149), which are in general too large to use any other route, pass from mother to embryo. The boundary of the breakdown is marked by the terminal sinus.

Gut, anterior intestinal portal, heart, and posterior intestinal portal are formed much as they are in the chick. Amniotic folds arise and arch over the embryo to form the amnion and chorion. the latter being continuous with the trophoblast. The allantois grows out from the gut, rapidly enlarges, and bulges over the posterior intestinal portal into the extraembryonic cœlom. The splanchnic mesoderm with which it is covered joins the somatopleure of the trophoblast with which it comes in contact, and puts out processes which burrow into the wall of the uterus. The resulting structure is the chorioallantoic placenta (Fig. 28.28 E), comparable with the chorioallantoic membrane of the chick.

A comparison of Fig. 28.28 D with Fig. 28.24 C will show that at this stage, about 5 days after fertilisation, the embryo of the rabbit is very similar to that of the chick at about 7 days of incubation. There is no yolk, but the hypoblast has come to enclose the fluid of the blastocyst and forms a yolk sac. Heterochrony, the phenomenon of the appearance of a series of structures at different times and in different temporal relations to each other, is well shown, the chorion of the rabbit, for example, being complete before any other membrane of the embryo itself appears,

while in the chick it is not formed until after the embryo is well established.

The placenta grows and becomes a complicated structure to which villi from the uterus contribute. Embryonic blood vessels grow into the allantois and the walls between these and the

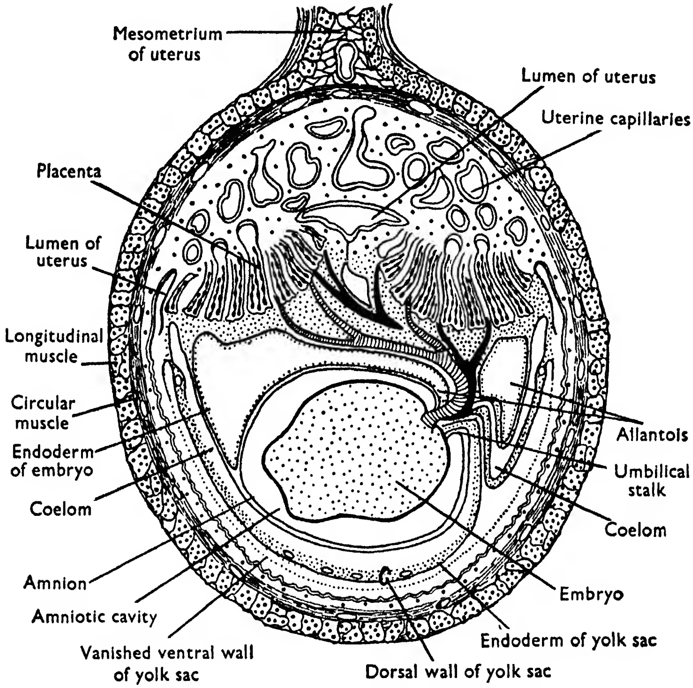


FIG. 28.29.—Transverse section of the uterus of a rabbit with an embryo of the 19th day.—Partly after Marshall.

uterine blood vessels become very thin, so that foodstuffs and oxygen can pass from mother to embryo, and carbon dioxide and other excretory products in the opposite direction An embryo nourished in this way is a fœtus.

The necks of the yolk sac and allantois with their contained blood vessels and the surrounding body wall become narrowed down to an umbilical stalk, and after four weeks the fœtus is forced out of the mother's body by contractions of the uterus in the process of birth. The umbilical stalk ruptures, leaving a mark, the umbilicus or navel, on what is now the ventral surface of the abdomen, and the placenta is shed as the afterbirth.

EARLY DEVELOPMENT OF OTHER MAMMALS

Other mammals show variants on this story, and heterochrony is marked. Fig. 28.30 shows early embryos of marsupial, mouse and rhesus monkey.

In the marsupials the embryonic disc develops from the actual

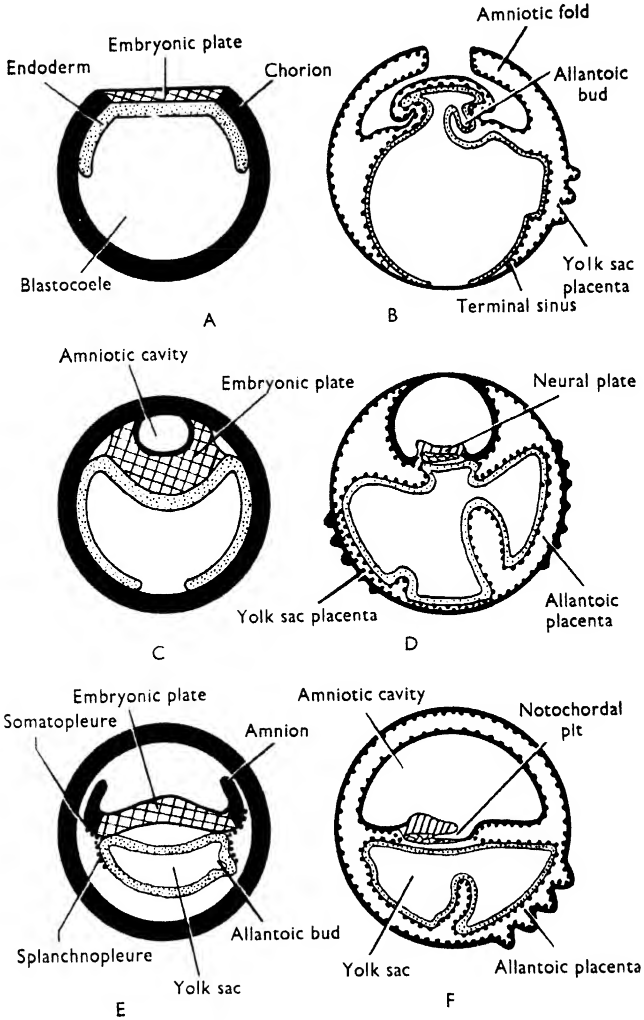


FIG. 28.30.—Diagrams of early development of mammals, sagittal sections. *A*, *B*, marsupial; *C*, *D*, mouse; *E*, *F*, primate.

surface of the trophoblast and there are no cells of Rauber; the allantois does not reach the chorion, and the embryonic part of the placenta is formed only from the somatopleure of the latter and the splanchnopleure of the yolk sac.

In the mouse the amnion is formed precociously as the wall of a cavity that appears in the inner cell mass when the hypoblast cells begin to migrate from it. The primitive streak is formed on the floor of this cavity, so that the embryo is never exposed to the uterine lumen, a phenomenon called entypy of the germ. It is probable that some of the extraembryonic endoderm is derived directly from the trophoblast wall instead of from the inner cell mass.

In the primates also there is entypy, and much of the extra-embryonic endoderm and mesoderm, including the yolk sac and allantois, arises directly from the trophoblast. The primitive streak provides mesoderm only for their stalks and for the embryo. There is no node of Hensen, but in its place is a pit, with a dorsal lip overhanging a tube that leads to the space that will form the future gut, a situation very similar to that in reptiles. The cells that roll in at the pit form notochord; since the endoderm is not yet complete in the midline, this is reminiscent of what happens in the frog, where the notochord for a time forms the roof of the gut.

In man (Fig. 28.31) all the embryonic membranes, with their mesodermal components, are almost complete before the embryo is formed.

ENDOCRINE CONTROL

The formation of the maternal part of the placenta, like the rest of the sexual cycle, is under the control of a complicated series of hormones produced by the pituitary gland and the reproductive organs.

The stimulus that starts the cycle in the female is a seasonal change in the outside world. In most mammals it is the increasing intensity of light or length of day in spring, acting through the eyes, and it probably causes the hypothalamus of the thalam-encephalon to secrete a hormone which travels in the hypophyseal portal system to the anterior pituitary. In other mammals, such as sheep and cattle, the reverse light-changes have the same effect, so that breeding takes place in autumn. The anterior

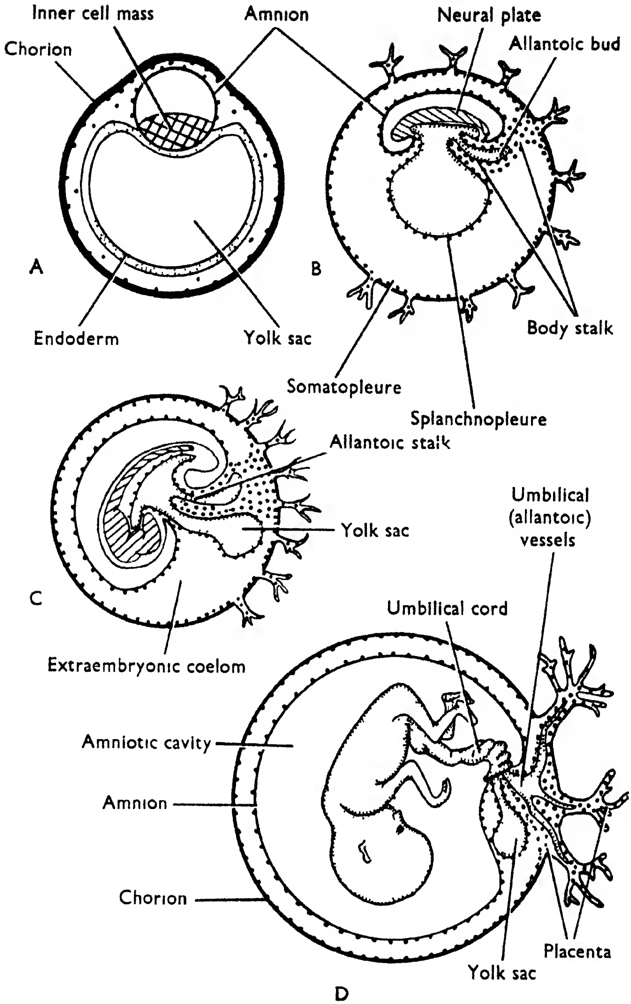


FIG 28 31 -Development of man *A*, diagrammatic sagittal section of early blastocyst the extraembryonic mesoderm has been produced from the chorionic wall, and the yolk sac and amnion are becoming invested with it before the appearance of the primitive streak , *B*, diagrammatic sagittal section of later stage, with primitive streak and allantois, whose splanchnopleure is from the first continuous with the chorionic somatopleure forming the body-stalk , *C*, diagrammatic sagittal section showing the expanding amniotic cavity ; *D*, embryo of about 3 months, attached to the uterus — After Nelsen, *Comparative Embryology of the Vertebrates*, 1953, Blakiston, New York

pituitary is stimulated to produce two hormones. The follicle-stimulating hormone (FSH) causes the maturation of one or more Graafian follicles and also the secretion of the hormone œstrogen by the ovary. Oestrogen induces the phenomena of œstrus, and also reduces the activity of the pituitary in secreting FSH, so that no more follicles ripen. In many mammals the second or luteinising hormone of the pituitary (LH) is present in large enough quantities to cause ovulation when the follicle is ripe, but in the rabbit and some others it is liberated in sufficient amount only after copulation. In all, it causes the transformation of the follicle into the corpus luteum. This produces another hormone, progesterone, which prepares the uterus and vagina for the attachment of the fœtus and birth, causes the development of the mammary glands, and inhibits œstrus and ovulation. The maintenance of the corpora lutea is brought about by prolactin, a third or luteotropic pituitary hormone (LTH), which stimulates milk production also.

DEVELOPMENT OF INVERTEBRATES

The development of invertebrates does not differ in principle from that of vertebrates, though it is often very different in detail. Brief reference has already been made to that of *Hydra* (p. 97), *Obelia* (p. 104) and the sea-urchin.

The polychætes have eggs in which determination occurs very early—immediately after fertilisation—and it is accompanied by movements and visible specialisations in the cytoplasm (Fig. 28.32 A and B). A characteristic feature of many species is the extrusion and withdrawal of a polar lobe of cytoplasm before the cell divides (Fig. 28.32 D). Cleavage is of a peculiar kind called spiral, in which each cell has a predetermined fate (p. 638 and Fig. 28.33). The first division is vertical and divides the egg into right and left halves. The second is also vertical, at right angles to the first, so that there are four blastomeres lying approximately in the same plane. They are called, viewed from the cytoplasmic pole and read in a clockwise direction, A, B, C, and D. In *Pomatoceros* (an excellent example for class study) and other forms the aggregated pigment and much of the yolky material that was extruded in the polar lobe lie entirely in D, which is often larger than the others.

The third division occurs at the same time in all four cells,

and is at an oblique angle to the first two and slightly above the equator, so that four smaller micromeres, numbered 1a to 1d, lie above four larger macromeres, 1A to 1D. The micromeres do

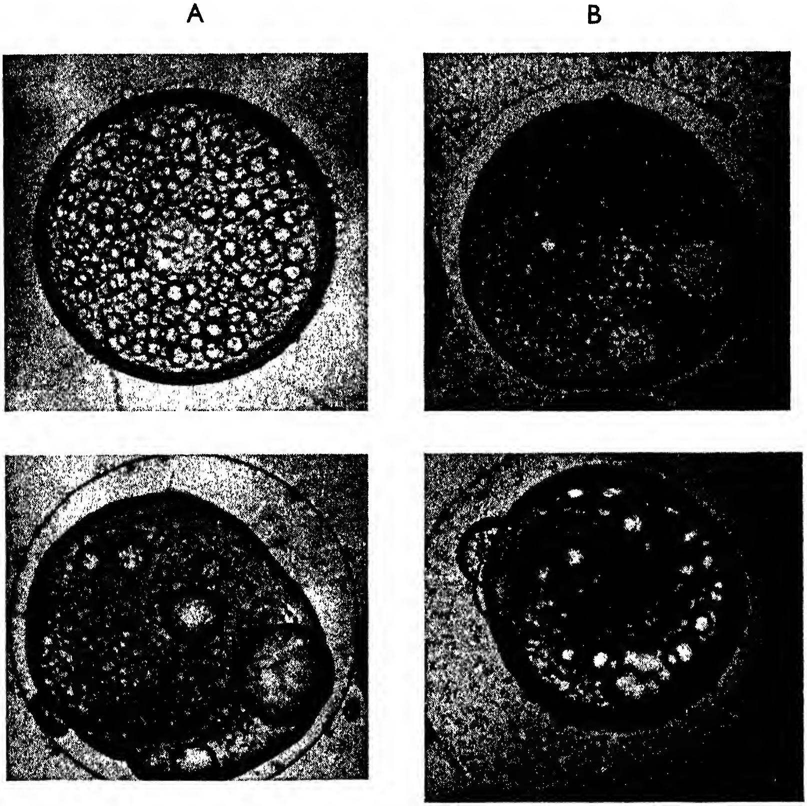


FIG. 28.32.—The eggs of polychætes. *A*, *Nereis*, immediately after fertilisation: the light space in the centre is the nucleus, the smaller spheres are yolk ; *B*, *Nereis*, slightly later: the fertilisation membrane has been raised up, and the yolk is aggregating into larger spheres at the pole opposite the point of entry of the sperm ; *Nereis*, later still, with the same events more marked : the compressed sphere under the fertilisation membrane at 7 o'clock is a polar body ; *D*, another polychæte, showing cytoplasmic differentiation and a polar lobe.

not lie directly above the macromeres, as do the corresponding blastomeres in the 8-celled stage of the sea-urchin or *Branchiostoma*, but alternate with them, each micromere lying clockwise to its macromere when the embryo is viewed from the cytoplasmic

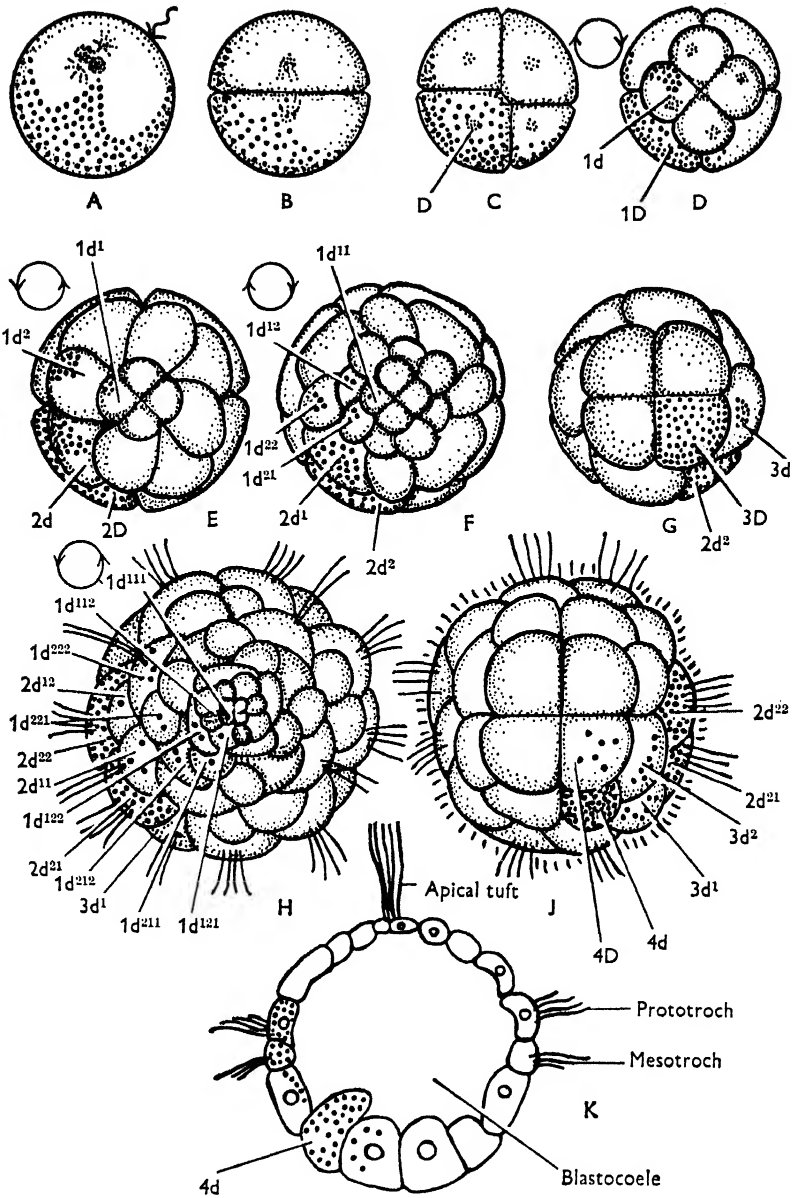


FIG. 28.33.—Diagrams of spiral cleavage. *A*, 1 cell, *B*, 2 cell, *C*, 4 cell, *D*, 8 cell, *E*, 16 cell and *F*, 32 cell stages all viewed from the cytoplasmic pole; *G*, 32 cell stage from the yolky pole; *H*, 64 cell stage from the cytoplasmic pole; *J*, 64 cell stage from the yolky pole; *K*, vertical section through 64 cell stage. The cytoplasm that goes into quadrant *D* of the 4 cell stage is stippled. Only the descendants of that cell are labelled. Note in *H* the position of the descendants of 2d, and in *J* the position of 4d.

pole; from this arrangement comes the name spiral cleavage (Fig. 28.33).

The next division, to attain 16 cells, is anticlockwise and synchronous; 1a, 1b, 1c, and 1d, or in general 1q, divide to give $1q^1$, and $1q^2$, the four cells $1q^1$ being around the cytoplasmic pole; the four cells 1Q divide to give 2q and 2Q, the former above the latter and smaller, and called the second quartet of micromeres. The next division, to give 32 cells, is clockwise, and produces the following quartets: $1q^{11}$, $1q^{12}$, $1q^{21}$, $1q^{22}$, $2q^1$, $2q^2$, 3q, and 3Q. This nomenclature is shown in Fig. 28.33. The next division, to produce 64 cells, is once more anticlockwise, and is usually the last to be synchronous. The quartets are now: $1q^{111}$, $1q^{112}$, $1q^{121}$, $1q^{122}$, $1q^{211}$, $1q^{212}$, $1q^{221}$, $1q^{222}$, $2q^{11}$, $2q^{12}$, $2q^{22}$, $3q^1$, $3q^2$, 4q, 4Q. At this division most of the pigmented material may be seen to be localised in 4D, although some of the other special protoplasm from macromere D has been lost into micromere 2d and its descendants. The four macromeres 4Q are extremely yolky and are destined to form the gut of the embryo and the adult; very often they are delayed in their next division relative to the other cells, so that at this division, which is clockwise and should produce 128 blastomeres, the ordered system begins to break up.

The embryo is now an early trochophore larva (p. 178) and in its further development each characteristic part (girdle, apical tuft, gut and so on) will be derived from a definite single cell or a related group of cells of the 128 cell stage. The whole of the mesoderm, for example, is formed from 4d. The changes by which these cells become the larval organ are merely spatial re-arrangements, and so far as is known no inductions occur.

In terrestrial annelids, such as the earthworm, there is no trochophore, and there are other simplifications, but the development is recognisably derived from spiral cleavage (Fig. 28.34). A blastula invaginates to form a gastrula, along whose ventral surface the mesoderm comes to lie as two bands, each formed by the division of a ‘ pole cell ’ at the hind end which was determined early in cleavage and corresponds to 4d in *Pomatoceros*. Each band subsequently divides into a row of mesoblastic somites, which become hollow. The cavity of each somite communicates with that of its fellow on the other side of the body to form the cœlom of one segment.

The typical early molluscan development is very similar to

that of polychætes, with spiral cleavage and a trochophore. There is, however, a little less determination, and some epigenetic events, such as the induction of the shell-gland by the gut, occur at later stages.

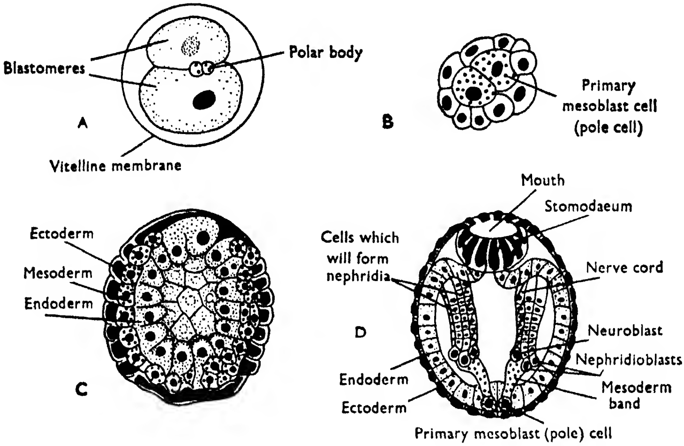


FIG. 28.34.—The development of an earthworm. *A*, 2-celled stage ; *B*, blastula; *C*, gastrula in ventral view ; *D*, late gastrula in ventral view : the blastopore has narrowed down to become the mouth.—After Wilson.

The crayfish has a peculiar form of incomplete cleavage, in which a layer of cytoplasm and nuclei, in which cell-walls are later laid down, comes to surround a mass of yolk (Fig. 28.35).

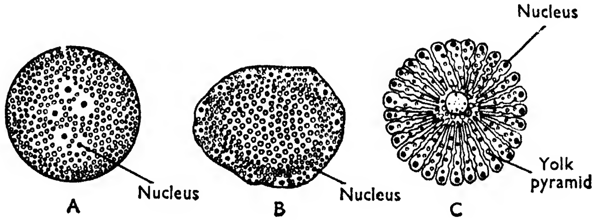


FIG. 28.35.—Three stages in the cleavage of the egg of a crayfish.—After Parker and Haswell.

This stage possibly corresponds to the blastula, the blastocœle being replaced by or filled with yolk. A ventral groove invaginates to form the gut, and the mesoderm is formed from two ventral bands, without pole cells. Mesoblastic somites are formed, but their cavities afterwards disappear except in the segment of the antenna, where they persist as the cavities of the green glands,

the only part of the cœlom that remains in the adult. In this development some of the epigenetic processes are left, as in vertebrates, until after cleavage.

The development of insects is aberrant, but can be derived from that of the crayfish. The lozenge-shaped egg contains two specialised regions of cytoplasm, the fertilisation centre containing the nucleus, and the activation centre. Migration of the nucleus during and after fertilisation, and interaction between the nucleus (or daughter nuclei) and the activated cytoplasm, are necessary for the organisation of the embryo. Development ranges from indeterminate to highly determinate.

The development of tunicates is determinate, and the organisation is in some species largely made visible by the distribution of pigment, even before fertilisation (Fig. 28.36).

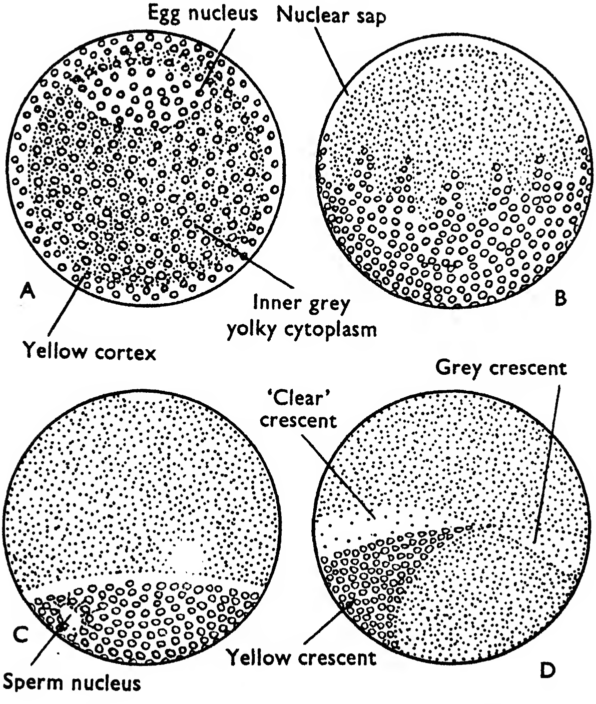


FIG. 28.36.—The egg of the tunicate *Styella*, drawn in partial transparency, showing the cytoplasmic movements that occur after fertilisation. *A*, before fertilisation; *B*, immediately after fertilisation: the nuclear membrane has burst, and the nuclear sap is extending, while the yolky cytoplasm is accumulating at one pole; the clear cytoplasm is beginning to form a band above the sperm nucleus; the nuclei have met and cleavage is about to take place: the cytoplasm is now in four bands above the yolk.—Based on Conklin.

SUMMARY

The process of development is inevitably complicated; the individual begins as an egg, which is structurally a single cell, and ends as a vertebrate or insect or whatever it may be. It is not surprising therefore that, since they start from the same point, embryos resemble each other more or less for some distance along the road which they travel, and that the greater the final resemblance of the adults, the longer does the similarity of the embryos persist. Thus while resemblance between a vertebrate and a mollusc is lost soon after cleavage, a 7-day chick and a 5-day rabbit embryo are closely similar. For some days more the rabbit can hardly be distinguished from other mammals, then it becomes recognisable as a lagomorph (p. 484) and finally as its own species. The sex of an animal may be indistinguishable until long after it is fully grown, and even then, as in many birds, only by its behaviour or by dissection. Further, there may be some degree of resemblance between the embryo of one animal and the adult of a structurally simpler type. For example, a typical gastrula, such as that of *Branchiostoma*, has a formal resemblance to *Hydra*, although it differs much in detail—the endoderm cells are not digestive, there are no tentacles, and so on; the embryos of amniotes possess visceral clefts, which are found in fishes not only in the embryos but also in the adults.

In the first place, the species of the animal, and many of its infraspecific characters, are determined by the genes in the chromosomes (Chap. 29), and although the maternal cytoplasm sometimes plays an important part, this in its turn is determined largely by the chromosomes under the influence of which it was formed. It is obvious enough that the genes can only act in an appropriate physical and chemical environment—a hen's egg will not develop unless it is kept warm, nor a frog's unless it is in water—but the external control is much closer than this, as small variations may cause alterations in the form of the embryo; for example, the addition of magnesium salts to the sea water in which they normally develop causes fish embryos to develop a single eye in place of their normal two. At much later stages the environment may still be an important determinant; for example, the larvæ of many marine bottom inverte-

brates only metamorphose when they receive the mechanical stimulus of a suitable substrate for the adult.

At least up to a late stage in development the division of the nucleus at each cell division is mitotic (p. 696) and equal, so that the differentiation of cellular type is not directly due to differentiation of the chromosomes, and it is very unlikely that any process akin to mutation (p. 729), which is rare and irregular, could take place with the frequency and regularity with which embryonic cells change their form. Yet cells, as we have seen in Chapter 26, acquire irreversible characteristics, so that it seems that there must be important changes in the cytoplasm. The only other possibility is that the chromosomes change under the influence of their environment; this cannot be disproved, but where, as in many of the lower animals and in almost all plants, regeneration of a whole organism can take place from a piece of specialised tissue, it is unlikely, and any suggestion that the nucleus can be altered in any regular way by outside influences is rejected by modern geneticists. We must therefore seek factors which can influence the cytoplasm, and some of these are known.

We have already seen that the earliest specialisations of the embryo are its main axes, and that these are determined by accidents of position. In animals with determinate cleavage irreversible specialisations occur within the egg, but even with indeterminate cleavage it is still the position of a cell relative to others that determines its fate. The important groups of cells are the organisers. In vertebrates (and especially Amphibia, where it is best known) the fundamental organiser is the dorsal part of that region of the blastula which is going to form endoderm and mesoderm, and in particular that part of it which forms the prominent dorsal lip of the blastopore. Wherever these cells are they will form the proper structures, and they induce the cells which surround them to arrange themselves in the appropriate way to form the other parts of the body. If the dorsal lip is cut out of a blastula and grafted in at another spot, its cells invaginate at their new position and an embryo is formed which has quite different axes from those it would have had if the operation had not been performed. If the dorsal lip of one blastula is grafted into another which already possesses its own, invagination takes place at two points, and a double monster is produced (Fig. 28.37). After the cells have been under the influence of one organiser for some time their fate becomes

fixed, and cannot be altered by the introduction of another organiser in a different relationship. Besides the main organiser there are a number of subsidiary ones ; the myotome, for example, induces the formation of a ventral nerve root in the tissue above it. Where an organiser from one species is grafted into the embryo of another it may still be able to induce organ development, but

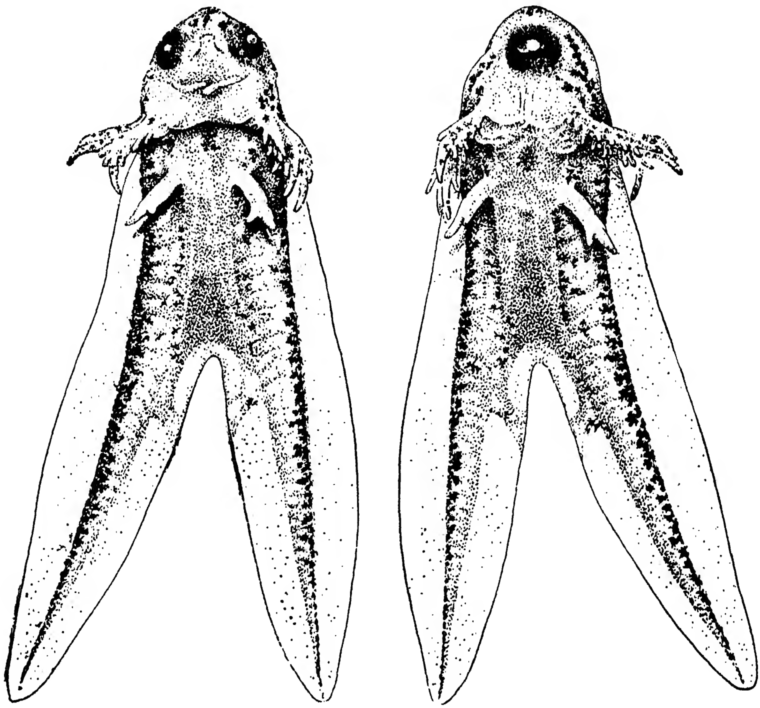


FIG. 28.37.—Newt monsters, formed by grafting together two gastrula halves. The anterior regions (seen in ventral view) have a plane of symmetry at right angles to that of the posterior regions (seen in side view). The monster on the right has a single eye.—From Huxley and De Beer, after Wessel.

the details of the tissues produced, as distinct from their type, are those not of the organiser but of the host, showing that the genes of the latter are still active.

The mechanism of action of the organiser is obscure. There can be no doubt that its cells have acquired some properties which are not easily lost, for if all the cells of a gastrula of *Amblystoma* are separated by treatment with mild alkali, stirred, and then neutralised, they will rearrange themselves with the

mesoderm going to the interior and the ecto- and endoderm-forming surface epithelia ; organs such as the notochord, somites and kidney are subsequently formed. The processes which take place seem to be a movement of cells similar to that of gastrulation and possibly caused by surface forces, adhesion of like cells, and induction. The action of the organiser in initiating gastrulation can be imitated by a wide variety of tissues, both living and dead, by many chemical substances, and even by extreme temperatures. Any chemical substance that induces development in other cells is called an evocator. The simplest seems to be a salt solution which induces a mild cytolysis, and it is probable that many of the more complicated substances act in the same way. The action of the cytolysis may be to liberate within the reacting cell substances, previously combined and inactive, which then determine the fate of the cells as nerve cells, ectoderm cells, or whatever it may be. According to this view the labile tissues must contain substances which can cause them to develop in various ways ; it is an accident of time and place which is liberated and so has its effect. The substances concerned, though present in the cytoplasm, are perhaps akin to genes.

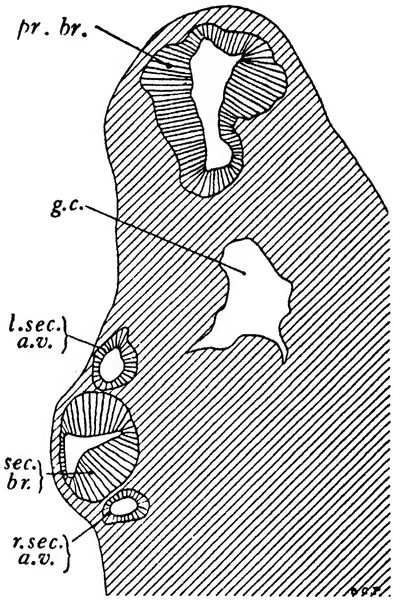


FIG. 28.38.—Section through an organiser-graft in the newt *Triton*. The anterior end of the secondary embryo is at right angles to the long axis of the primary embryo.—From Huxley and De Beer, after Spemann.

g.c., gut cavity ; *l.sec. a.v.*, left ear vesicle of secondary embryo ; *pr. br.*, brain of primary embryo ; *r.sec. a.v.*, right ear vesicle of secondary embryo ; *sec. br.*, brain of secondary embryo.

In some instances the effect of an organiser is to suppress a development that would otherwise take place. Thus if the presumptive notochord cells are removed, presumptive somite cells become notochord, so that it seems that the first cells to become notochord suppress the change of other mesoderm cells into what might be called their first choice. Inhibition of a comparable

sort is well-known in plants, where an active stem-apex suppresses the development of lateral buds below it.

That which a group of cells ordinarily does become is called its potency ; the whole range of possibilities open to it is its competence. The results of all these interactions depend on at least three features : first the tissues involved must be in definite spatial relationships to each other ; second, the organising tissue must produce an evocator which is a meaningful cue for the reacting tissue ; and third, the reacting tissue must be competent to respond. The reaction to evocator may be a graded response, but more often it is a threshold effect, so that until a certain concentration of evocator is reached there is no response, but above this concentration the response is complete. Sometimes a competent tissue reacts differently to two or three separate thresholds of one evocator. For example, it seems that in some animals, such as the frog, the whole neural tube is evoked by one substance, which is produced copiously at the anterior end in the prechordal plate, but whose concentration diminishes progressively as one goes towards the posterior end. The line of demarcation of brain and spinal cord is evidence of two different thresholds of the reacting tissue. In other forms, for example the chick, two substances whose concentration gradients are inverse seem to be involved ; brain evocator has a high concentration anteriorly and spinal evocator a high concentration posteriorly. It is possible that neural crest tissue is induced by a low concentration of spinal evocator.

After the primary organisation has resulted in the differentiation of the primary tissues (notochord, prechordal plate, somites, nerve cord and brain, and often gut and skin) each of these in its turn organises neighbouring tissues so that still greater complexity is achieved and the whole embryo with all its functioning organ systems results.

The later development of tissues is controlled, so far as we know, in two ways. The first, which has some resemblance, which may only be superficial, to the control by organisers, is by the action of specific chemical substances or hormones which circulate in the blood or diffuse through the tissues to affect cells other than those which produce them. Examples of hormones have been described in earlier chapters; thyroxine and the growth factor of the anterior pituitary affect growth in size and proportion, and also have specific effects on amphibian metamorphosis. Thyroxine

administered to young fish of the genus *Periophthalmus*, an animal of the East Indies which comes out of the sea and walks on land, breathing through its tail, causes them to exaggerate their terrestrial adaptations, and the pectoral fin comes to resemble a pentadactyl limb. It looks as if the fish had the potentiality of becoming a tetrapod, which only needed liberating just as the organiser liberates the substance in amphibian blastula cells which enables them to form a nerve cord. The differential development of the kidney ducts in male and female vertebrates depends on hormones from the testis; the pronephric duct becomes an oviduct unless it is suppressed, while the mesonephric duct forms a Wolffian duct only if male hormone is present.

Lastly, much of the detailed development of an organ or a tissue depends on its continued use. Muscles become bigger when they are continually stimulated to contract, skeletal tissues grow where the body is most subject to strain, and the blood vessels in the chick enlarge in proportion to the speed at which blood flows through them.

There seem then to be six influences which determine the form and function which any cell will finally have. (1) The genes which it inherits from its parents. Rarely, as in the red blood cells of mammals and in epithelia where division of the nucleus is amitotic (p. 702) these, having done their work, may abdicate from any further influence. It seems that many of the adult tissues of mammals have different numbers of chromosomes; if this is so part of their differention might be due to the different genes which they receive. (2) The external environment, which co-operates with the genes. (3) The position of the egg in the ovary, or relative to the sperm at fertilisation, which determines uneven distribution of substances within the cytoplasm. (4) The position of some cells relative to others, which by virtue of their special contents are dominant and impose a pattern on their neighbours. (5) Hormones liberated by special parts of the body, and (6) use and disuse. Each of these acts on a partial differentiation produced by its predecessors in the hierarchy, and the differentiation is progressively and rapidly increased.

29

HEREDITY AND CELL DIVISION

MENDEL'S EXPERIMENTS

THE first man to carry out experiments on heredity which gave clear results was Gregor Johann Mendel, a teacher of physics in the school of the Königskloster at Brünn in Austria (now Brno in Czechoslovakia), an Augustinian house of which he was afterwards Prälat or Head. His chief work extended from 1857 to 1865, and was published in 1866 ; it dealt with a plant, the garden pea *Pisum sativum*, but must be described even in a zoology book because of its fundamental importance.

Mendel introduced into his work three new principles, which were the foundation of his success. (1) He worked with pure lines, which had been inbred for long enough for it to be clear that, if they were not crossed, they did not vary significantly in the characters under investigation. His choice of the garden pea was determined by the fact that, since it is normally self-fertilising, it is protected from accidental crossing. (2) He chose characters (or character differences) which were clear-cut and distinct, not those, such as height or intellect in man where there is a continuous gradation, or coat colour in dogs where the variety is bewildering. He used twenty-two varieties of pea obtained from seedsmen, but these could be classified as differing only in one or more of seven pairs of characters, and it was to these character pairs, not the whole appearance of the plant, that his attention was given. (3) He kept careful statistical records of the progeny of each individual cross in each generation.

His results may be illustrated by the crosses between tall and dwarf plants. The former are 6 to 7 feet high, the latter 9 to 18 inches, so that although there is some variation in height within each pure line there is no overlap between the two. The anthers of the flowers of one plant were carefully removed from the bud, and pollen from the other placed on the stigma ; crosses were carried out in both directions, so that the tall and dwarf parents provided pollen in turn. In thirty-seven experiments on ten plants he found that the hybrid seeds developed to give tall plants, and nothing but tall plants, whichever way the cross was made. The character tallness he therefore called ***dominant***,

and shortness, which had disappeared in what is now called the first filial, or F_1, generation, he called *recessive*. The next thing was to breed from the F_1 generation by allowing the plants to self-pollinate. In the second filial generation, or F_2, Mendel grew 1,064 plants, and of these 787 were tall, and 277 dwarf; the recessive character had thus reappeared in approximately one-quarter of the grandchildren of the original parents. In the F_3 generation the dwarfs from the F_2 gave nothing but dwarfs, while of 100 F_2 talls 28 gave only talls, and 72 gave both talls and shorts in the approximate ratio of 3 : 1. The crosses involving the other characters gave similar results and similar ratios, the larger the number of results the closer being the ratio to 3 : 1. Mendel was thus able to state as a rule for the pea crosses that when the hybrids form seeds they do so in the proportion of one which is a pure dominant to one pure recessive to two hybrids. He carried some of his experiments through seven generations from the original parents, getting similar results each time, from which he deduced that the hybrids would never become pure. The pure dominants and recessives are now called collectively homozygotes, and what Mendel termed hybrids are now known as heterozygotes. His experiments may be summarised in the form of a genealogical table; capital letters stand for the dominant character, lower-case for the recessive, and the two together for the hybrid. For reasons which appear later, it is better to represent each homozygote by a double letter.

			AA x aa		
F_1			Aa		
F_2	AA $\frac{1}{4}$		Aa $\frac{1}{2}$		aa $\frac{1}{4}$
F_3	AA	AA $\frac{1}{4}$	Aa $\frac{1}{2}$	aa $\frac{1}{4}$	aa
			and so on		

The next step that Mendel took in the analysis was to find out what happened when the parents differed in two or three pairs

of contrasting characters, and he found, in all the combinations which he tried, that the pairs were inherited independently. The F_1 generation showed only the dominant characters, but on self-pollination an F_2 was produced which contained all the possible combinations of characters in the approximate proportions given by multiplying together the F_2 ratio for the different pairs of characters. For a cross between plants from round and yellow seeds (dominant) and plants from wrinkled and green seeds (recessive) the F_2 consisted of

315	round yellow seeds
101	wrinkled yellow seeds
108	round green seeds
32	wrinkled green seeds

Further breeding showed that of these only the wrinkled green seeds, thirty-eight of the round yellow seeds, and about the same numbers of the new combinations wrinkled yellow and round green, bred true ; the others were heterozygous for one or both characters. If we represent the plants homozygous for roundness by RR, for yellowness by YY, the corresponding recessives by the lower-case letters, and the heterozygotes by Rr and Yy, the numbers of the F_2 come out as shown in Table XI, column 1,

TABLE XI.

38	RRYY	1/16	33
60	RrYY	1/8	66
28	rrYY	1/16	33
65	RRYy	1/8	66
138	RrYy	1/4	132
68	rrYy	1/8	66
35	RRyy	1/16	33
67	Rryy	1/8	66
30	rryy	1/16	33
529		1	528

which excludes a few which did not live. Column 3 shows the fractions obtained by multiplying together the separate ratios ($\frac{1}{4}$ RR + $\frac{1}{2}$ Rr + $\frac{1}{4}$ rr) and ($\frac{1}{4}$ YY + $\frac{1}{2}$ Yy + $\frac{1}{4}$ yy) already known for the single pairs, and column 4 these fractions of the total, to the nearest whole number. It will be seen that the agreement is close.

Mendel did not stop at experimenting, but tried to find a theoretical basis for his results. He saw that this must lie in the nature of the sex cells, and that these must have a constitution which is connected with that of the parent which forms them and with that of the offspring to which they give rise, but is not necessarily the same as either of these. He enunciated a single principle :

> ' the pea hybrids form egg and pollen cells which, in their constitution, represent in equal numbers all constant forms which result from the combination of the characters united in fertilisation '.[1]

He used this to predict the results of what are now called back-crosses (i.e. crosses between hybrids and their pure-breeding parents). Experiments confirmed the prediction, so that the principle was verified in the classical way for testing a scientific hypothesis. Mendel speaks of the principle as ' the law governing *Pisum* ', but he was much too good a scientist to generalise it to other organisms, and states that this must be the subject of further experiment. Unfortunately his own further work, on the bean *Phaseolus* and the sunflower *Hieracium*, met difficulties, and after promotion to the headship of his House he had no time for investigation.

Although Mendel's papers must have been seen by many of the leading biologists of the time, their importance was overlooked, and it was not until 1900, as a result of a deliberate search through the literature for anything that might throw light on the problem of heredity, that they were rediscovered. His results were soon confirmed for other plants, and extended to animals by Bateson in Cambridge. Absence of horns, as in the redpoll and other breeds of cattle, is dominant to the horned condition, normal fur in rabbit and guinea-pig is dominant to Angora, and normal plumage in fowls to the condition known as silky, in which the barbules are deficient. It was, however, found that dominance does not always occur ; the heterozygote may be exactly intermediate between the two parents, or resemble one rather more than the other. The bluish-grey Andalusian fowl,

[1] Quoted from the translation of Mendel's paper made by the Royal Horticultural Society, and revised and republished by W. Bateson in his *Mendel's Principles of Heredity* (Cambridge, 1909) p. 343. The fact that the pollen grain was not strictly the male cell was not known in Mendel's time, and the term gamete had not been invented.

which was imported from Spain in about 1850, was for long a trouble to breeders, because many of the chicks came black or a peculiar white and grey colour ; we now know that the blue type is a heterozygote, and it can be produced by mating the black and white forms (Fig. 29.1.).

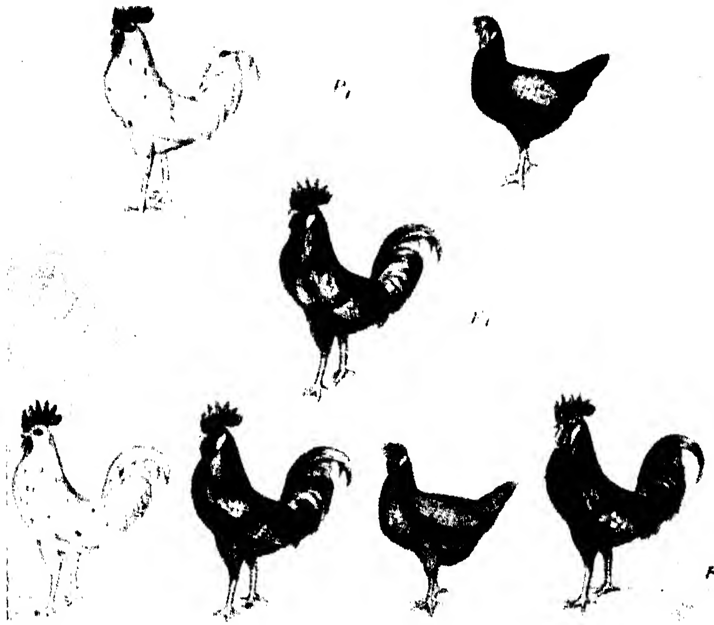


FIG. 29.1.—To illustrate the results of crossing two pure-bred (homozygote) races of Andalusian fowls.—From Morgan.

P_1, The parents, one splashed-white and the other black ; F_1, the first hybrid generation, all individuals of which are alike, of a bluish-black shade due to the blending of the colours of the parents ; F_2, the second hybrid generation, bred by mating F_1 individuals together. One quarter resembles each of the parents and the remaining half are like F_1.

It has long been customary to state the essential theory of Mendelism in two parts :

1. *Segregation.* Every gamete produced by a heterozygote contains unchanged either one or the other of any two factors determining alternative unit characters in respect of which its parental gametes differed.
2. *Recombination.* The factors determining different unit characters are recombined at random in the gametes of an individual heterozygous in respect to these factors.

These are ' Mendel's Laws ' of the textbooks, but they have in

practice, as we shall see later, many exceptions, so that they are not ' laws ' in the sense in which that word is used in physics ; nor were they enunciated in this form by Mendel, so that they are better known as the Mendelian principles. Mendel's own statement, which we have already given, combines the two in one rule which is shorter and perhaps more elegant than the common form. Mendel's essential discovery was that the characters of a zygote are determined by unit factors in the gametes from which it was formed. Nearly always a gamete contains, for a pair of alternative characters, only a single factor, and sometimes the distribution of the factors for one pair of characters is independent of that of factors for another pair. When these two conditions hold, the Mendelian principles are true.

Alternative characters of the type with which Mendel dealt are now generally said to be contrasted or allelomorphic, and the essential part of his theory is that a gamete carries a factor for only one character of such a pair, the factor being not the character itself but a material something which tends towards its production.[1]

When two gametes fuse to form a zygote two factors for a pair of contrasted characters come together ; if they are alike the result is a homozygote, dominant or recessive as the case may be, and if they are unlike the result is a heterozygote, which resembles the dominant or is more or less intermediate in appearance. It is obvious that we must distinguish between the appearance of the individual, which is now called the phenotype, and its inherited nature or genotype. Mendel's F_1 tall peas had the same phenotype as their tall parents, but were of a different genotype, as became clear when they were bred from. To forecast the results of any given breeding experiment we must know the genotypes of the individuals to be crossed ; alternatively, from the results of the experiment we may be able to determine the genotypes of the parents. In either case, the first thing to do is to set out the problem in the form of a genealogical tree and determine the factors which must be present in the gametes, which are the connecting links between the two generations. If the genotypes of the parents are known, and the possible gametes are of more than one type, the

[1] This is the sense in which Bateson, who invented the term, used ' allelomorphic ', but it is also applied to the factors, which are called allelomorphs or alleles, and some modern geneticists would restrict it to this usage. The context will usually show in which way the word should be taken

simplest way of finding their possible combinations in their correct proportions is to draw a rectangle subdivided into squares equal in number to the product of the numbers of kinds of gametes produced by the two parents. Thus in Mendel's experiment with round yellow and wrinkled green seeds the F_1, which were heterozygotic round yellows, must have been capable of giving gametes which carried the factors

RY
Ry
rY
ry

When we cross two of these plants we must therefore draw a rectangle with $4 \times 4 = 16$ squares (Fig. 29.2). The gametes of

RY RY	Ry RY	rY RY	ry RY
RY Ry	Ry Ry	rY Ry	ry Ry
RY rY	Ry rY	rY rY	ry rY
RY ry	Ry ry	rY ry	ry ry

FIG. 29.2.—'Chequer-board' or Punnett square for a two-factor cross, round yellow, and wrinkled green seeds.

one parent are then written into all the horizontal rows, and of the other into all the vertical rows. The factors which now appear in each square represent a possible zygote. If like terms are collected (i.e. factors for the same pair of allelomorphs) it will be seen that the possible zygotes are in the proportions shown in Table XI, and when allowance is made for dominance, give the 9 : 3 : 3 : 1 ratio which Mendel actually found. What we have done by this 'chequer-board' is simply a piece of mechanical

multiplication. In the example given, the two parents were similar and so the resulting squares were regular, but the same method is used where the parents are different. Mendel, for example, tested his theory by a ' back cross ' of the heterozygote to one of the original homozygous parents. If this is the recessive, its only possible gametes are ry, and those for the heterozygote are the same as before. We have, therefore, a rectangle of 4 × 1 squares (Fig. 29.3), and it is clear that individuals of the genotype RrYy, Rryy, rrYy and rryy should be formed in approximately equal numbers. Mendel got in one experiment 31 round yellows, 26 round green, 27 wrinkled yellow, and 26 wrinkled green. It must be stressed that the mathematical ratios must not be exactly expected in practice, since they depend on random pairing of gametes, and on random sampling of the factors, and with small numbers there may be wide variations. This

RY ry	Ry ry	rY ry	ry ry

FIG. 29.3.—Backcross ' chequer-board '.

is especially important in animals where each litter is usually small. In a litter of eight guinea-pigs, bred from heterozygous normal/angora parents, for instance, one would not expect always to have six normals and two angoras ; five and three or seven and one would both be very probable, and even eight and nought or four and four not unlikely. But the totals of a large number of litters would approximate to a proportion of 3 : 1.

Although the main principles of Mendelism were confirmed by the early geneticists, they soon found that there were exceptions and difficulties. In particular, they found that different pairs of characters were not always independently inherited, or, in other words, that certain characters were associated together. There are two possible explanations of this : that the same factor determines more than one character, and that there are different factors but that they do not separate in the formation of the gametes. Each is sometimes true, but the second is the more important. Its discussion is best left until we have dealt with the cytological features of cell division.

MITOSIS

We have already mentioned that the active or dividing nucleus of a cell of a given species contains a set of chromosomes which are characteristic in number and appearance (Fig. 29.4). It is obvious that for this constant arrangement to be maintained there must be some special mechanism, and in fact in all normal cell division each chromosome divides longitudinally into two. Further, no chromosome ever arises, so far as is known, except by the division of a pre-existing chromosome. The process of division is called mitosis (formerly also karyokinesis), and will now be described (Fig. 29.5).

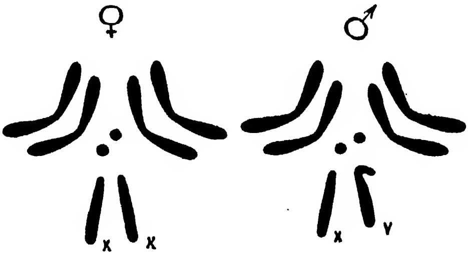


FIG. 29.4.—The chromosomes of the body cells of fruit-flies (*Drosophila*). Here there are only eight chromosomes, and the members of each of the pairs which separate at the reduction division can be recognised by their shapes and sizes.—After Morgan and others.

♀, The chromosomes of the female ; ♂, those of the male ; *X*, X-chromosomes ; *Y*, a chromosome which forms a pair with the single X-chromosome of the male, but is distinguishable from the latter by having a hooked end.

The first sign of activity in the nucleus is the division of the centrosome (p. 502), the halves of which travel to opposite poles of the nucleus. It is probable that division has at least begun much earlier, perhaps at the end of the previous division. Meanwhile chromosomes appear as relatively long, stainable threads ; close examination shows that each is double, and the half threads are called chromatids. The chromosomes shorten by contracting into a solenoid, and in so doing become thicker ; the nuclear membrane disappears, so that they lie free in the cytoplasm. This is the end of the first stage of mitosis, called prophase. The beginning of the next stage, or metaphase, is marked by the appearance of the spindle, a clear and unstainable region which lies across the cell between the centrosomes. In fixed cells the spindle appears to be made of fibres, and similar fibres, the astral rays, spread into the cytoplasm from the centrioles. The

meaning of this fibrous appearance is doubtful, but that the spindle is a real structure is shown by the fact that it can be pushed

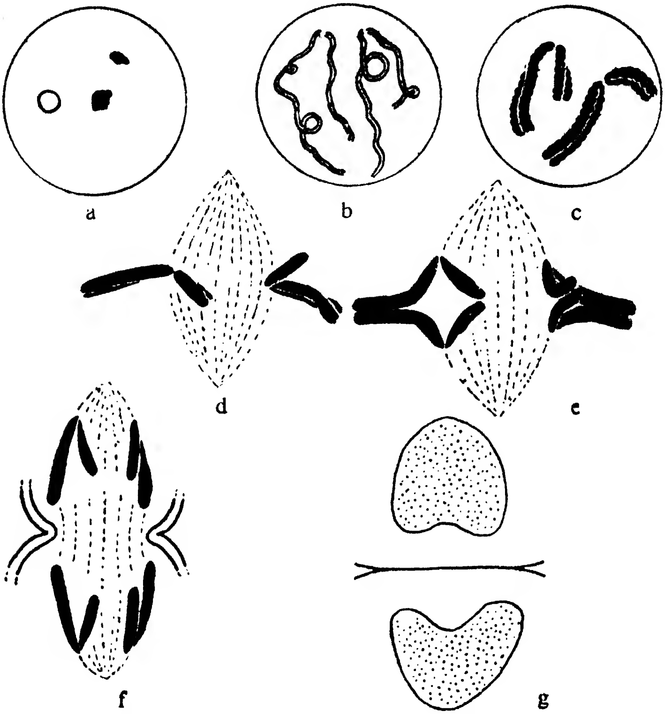


FIG. 29.5.—Schematic history of two homologous chromosomes during mitosis. From Callan, *New Biology*, No. 7, 1949. Penguin Books.

a, Resting nucleus surrounded by a nuclear membrane and containing a nucleolus and two aggregations of nucleic acid.
b, The chromosomes as they first appear inside the nucleus; each consists of two chromatids, and the centromeres are represented by gaps.
c, The chromosomes have contracted in length and increased in thickness (approaching end of prophase).
d, The nuclear membrane has disappeared, the spindle has formed, and the chromosomes lie with their centromeres on the equator (metaphase).
e, The centromeres have divided and are moving towards opposite poles of the spindle, carrying single chromatids with them (anaphase).
f, The spindle has elongated and the movement of the chromatids continues. The cytoplasmic cleavage furrow which will divide the cell into two is approaching from the sides.
g, The cleavage furrow is completed, and the daughter nuclei are being reconstituted; the chromatids have now become chromosomes (telophase).

about in the living cell by a micro-dissection needle. The chromosomes, now fully contracted, come to lie in a flat plate across its equator. Later behaviour shows that each chromosome is attached to the spindle at one point, and it is the position of this which gives the characteristic shape to the metaphase chromosome. At the beginning of the third stage, or anaphase, the part of the chromosome attached to the spindle, called the

FIG 29 6—First metaphase of meiosis in *Lumbricus terrestris* The chromosomes are near the surface of the egg × 370—Photo-[illegible]

FIG 29 7—Enlargement of a part of Fig 29 6 × 920—Photograph by Dr Muldal

FIG. 29.8.—Mitosis in male vole (*Microtus agrestis*) (2n=50), showing the giant sex chromosomes. The X is hook shaped. × 3,300.—Photograph by Dr. Muldal.

FIG. 29.9.—First prometaphase of meiosis in mouse (*Mus musculus*) (2n=40), showing the twenty paired bivalents. At the top the sex chromosomes, the Y less than half the size of the X. × 3,050.—Photograph by Dr. Muldal.

centromere, divides, and its halves move towards the poles. As each goes it takes with it the chromatid of which it is part ; in this way the chromatids are separated and become chromosomes. In the fourth and last stage, or telophase, the coils of the new chromosomes begin to unwind, and the nuclear membrane is reformed. The chromosomes finally become invisible and unstainable, and the nucleoli, which have disappeared in prophase, reappear.

The division of the cell takes place by the formation of a new cytoplasmic dividing wall in various ways. In amœboid cells in tissue culture the two daughter cells move actively away from each other, pulling out the cytoplasm between them to a narrow waist which finally breaks ; in eggs and early blastulæ there is a sudden rearrangement of the protoplasm and its surface, like the reverse of the way in which two soap bubbles in contact will suddenly become one ; in plants there is a slow laying down of a new dividing wall, and presumably something similar happens in epithelia.

The process of mitosis clearly provides for the maintenance of constancy of number and shape of the chromosomes, but it is to be noted that the really essential part, the division of chromosomes into chromatids, has never been seen, and must take place in the resting nucleus. We assume that the chromosomes continue their existence and identity while they are invisible ; there is no direct evidence for this, but much that is circumstantial.

MEIOSIS

There is another type of nuclear division, called meiosis (Fig. 29.10), or reduction division, in which the chromosomes split once for two divisions of the nucleus ; in animals, except for some Protozoa, it occurs in the formation of the germ cells from gametocytes. When the chromosomes appear in prophase they are not split into chromatids ; instead, and perhaps because of this, homologous or similar ones come together in pairs, sometimes for a short distance, sometimes for their whole length, and shorten and coil round each other to give the pachytene stage. Next comes the diplotene stage, in which the pairs fall apart except at certain points called chiasmata (singular chiasma). Each chromosome is now seen to be divided into two chromatids, and it is claimed that in a few instances it can be seen that at the chiasmata the chromatids

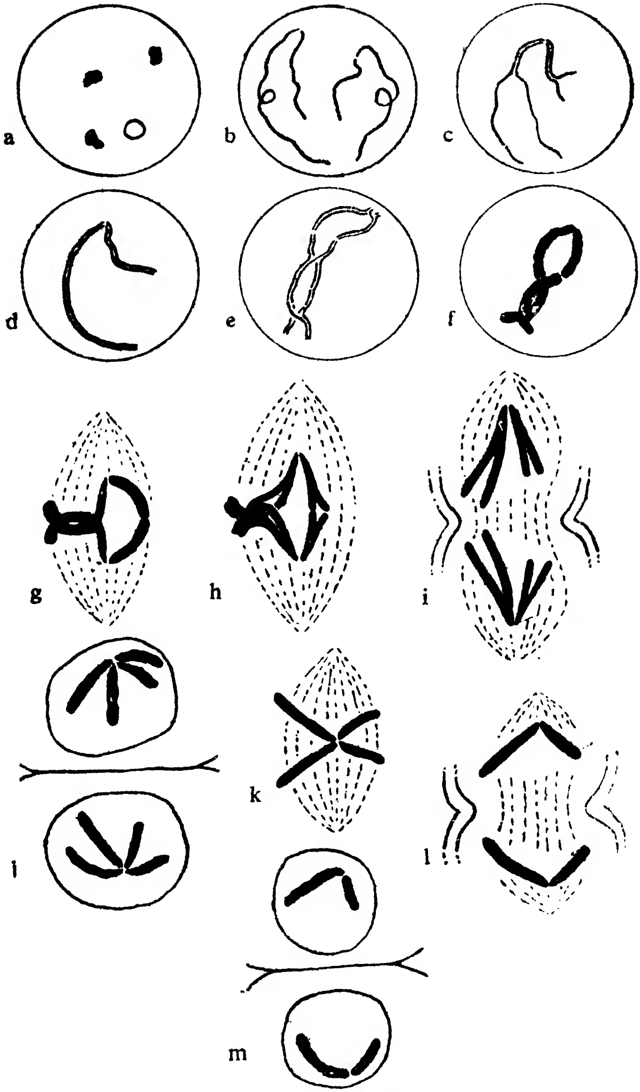


FIG. 29.10.—Schematic history of two homologous chromosomes during meiosis.—From Callan, *New Biology*, No. 7, 1949. Penguin Books.

a, Resting nucleus, with nuclear membrane, nucleolus, and three aggregations of nucleic acid.
b, The chromosomes appear; each is a single thread; the centromeres are represented by gaps.
c, The two homologous chromosomes have started to pair.
d, Pairing complete.
e, Each pairing chromosome has divided into two chromatids which have formed chiasmata at three points.
f, Shortening and thickening (approaching end of prophase).
g, The nuclear membrane has broken down, the spindle has formed, and the chiasmata are arranged on the equator (metaphase).
h, The centromeres are moving towards the poles, each pulling after it two chromatids (anaphase).
i, The spindle has elongated and the cytoplasmic cleavage furrow is approaching from the sides.
j, End of the first division; two nuclei have formed, and the cell has divided.
k, *l*, *m*, The second division is shown for one only of the products of the first division; the result is two nuclei with single chromatids.

exchange partners, a segment of one changing places with the corresponding segment of another, so that the separating chromosomes are not identical with those which come together. This phenomenon is called crossing-over. There follows uncoiling and shortening, and further repulsion of all parts of the chromosomes, especially the centromeres, except at the chiasmata, a stage called diakinesis. The other features of prophase take place, and then metaphase. In this there is no division of the centromeres, but those of the paired chromosomes move farther apart in anaphase and separate the chromosomes along their whole length. There is usually no telophase in the ordinary sense of the word, and the second division of meiosis may occur at once. Chromatids are already present, so there is no further splitting, but after the chromosomes are arranged on the metaphase plate the centromeres divide and the chromatids, which have now become chromosomes, are pulled apart. The result of the double division is four nuclei, each of which has only half the number of chromosomes of the original cell. The nucleus which has the full or double number (2n) is said to be diploid, that which has the reduced number (n) is called haploid, from a Greek word meaning single.

The first or heterotype division of meiosis leads in the female to the formation of the first polar body, in the male to the formation of the secondary spermatocytes. The second or homotype division leads to the formation of the second polar body and the spermatids, which grow to spermatozoa. In the female the first division is often complicated by cytoplasmic changes, such as the deposition of yolk during the pachytene stage. While this is going on the chromosomes may even disappear entirely, and some special stimulus, which may be the entrance of the sperm, is needed to complete the division. In mammals the end of prophase is normally reached before or just after birth, but the division is not finished until just before the egg is shed from the ovary in ovulation ; in man and other long-lived mammals meiosis may therefore take fifty years. In only a few species has complete meiosis been shown to occur in the adult.

AMITOSIS

In some cells there is an amitosis, where the nucleus just elongates and divides, without splitting of individual chromosomes. Sometimes this is pathological, but it is normal in the

meganucleus of Ciliophora and in many adult tissues, for instance in snails, insects, birds and mammals.

LINKAGE

We can now return to the later developments of genetics, which we left on page 695 with the statement that separate

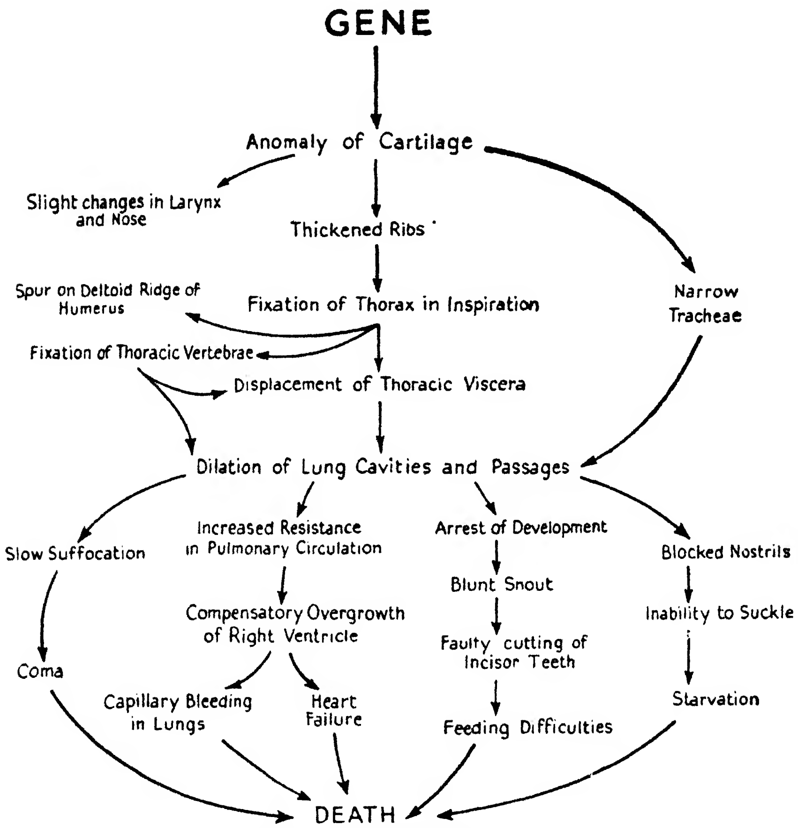


FIG. 29.11.—The pleiotropic effect of a single gene, grey-lethal, in the rat.—From Darlington and Mather, *The Elements of Genetics*, 1949. Allen & Unwin, London, After Grüneberg.

characters were not always independently inherited. Two types of connection must be distinguished ; in the first, two characters are always inherited together, and are quite inseparable. Here, a factor is having more than one phenotypic effect, and may be called pleiotropic. Generally, the multiple results follow from a single initial change, as in a large number of anatomical and

physiological defects in the rat, which were traced to a single anomaly in the formation of cartilage (Fig. 29.11), but it is not impossible that sometimes a single factor may determine more than one reaction, the effects of which would then be unrelated except through their cause. More often, there is merely a preponderance of one type of combination of the two characters, showing that the factors which cause them do not go into the gametes entirely independently. This, which is called linkage, was discovered in the sweet pea by Bateson and Punnett in 1902, but the great development of our knowledge of it followed the use as a breeding animal of the small grey fruit fly, *Drosophila*, and is due chiefly to Morgan and his school in New York from 1910 onwards.

In one of their experiments a wild-type fly, BBVV, was crossed with a form having two recessive characters, a black body and vestigial wings, bbvv, and gave a grey normal-winged heterozygous F_1, BbVv. Females of this were then back-crossed to bbvv males, giving this result

♀ BbVv x bbvv ♂

BbVv	bbVv	Bbvv	bbvv
586	106	111	465

On Mendelian principles equal numbers of the four types would have been expected, but instead, of the 1268 gametes formed by the heterozygous F_1 female, 1051 resemble those from which it was derived, and only 217 are the new combinations bV and Bv. Instead of 50 per cent. of the gametes being recombinations only 217 out of 1268, or 17.1 per cent are. Later experiments showed that, for a given pair of characters, this recombination value is roughly constant, and may have any value from 0 to 50. The former is a theoretical limit, which, if it is ever achieved, must be indistinguishable from the pleiotropic effects of a single factor.

CHARACTERS AND CHROMOSOMES

The position which we have now reached is that characters are passed from parents to offspring by factors contained in the

gametes in such a way that only one factor concerned with a pair of contrasting characters is present in a single gamete; that factors for different pairs of characters are inherited either independently or in such a way that there is a definite percentage association between two members of the pairs; and that, with this exception, the sorting-out and recombination of the factors in gamete production and mating is random. If each gamete contains one factor the zygote must contain two; there must be reproduction of these factors at cell division, and at some stage before the formation of the next generation of gametes there must be an orderly reduction of the factors in the cell to one.

It was pointed out by Sutton as early as 1903 that an obvious physical basis for all this was to be found in the chromosomes, but there were at first some difficulties. Now, however, the evidence for the connection is overwhelming, and its development is a pretty exercise in biological argument. Since, with rare exceptions, the results of reciprocal crosses are the same, we must look for the factors in the nucleus, for what little cytoplasm the male gamete contains often takes no part in fertilisation; in the nucleus, the chromosomes are the only things with any individuality, and their splitting before mitosis and reduction at meiosis provide a means of reproduction and segregation of the factors. But similarity is not proof of identity, and there is the objection that the continued separate existence of the chromosomes in the resting cell is an assumption, though a probable one; more evidence is needed, and is provided by the phenomena of linkage.[1] In all the organisms which have been deeply studied (it must be admitted that these are very few: half a dozen animals and rather more plants) it has been found that all the allelomorphic characters fall into groups, such that all the members of one group are linked together, and that the number of linkage groups is equal to the haploid number of chromosomes. The linkage is, as we have seen, not perfect, and departs from perfection by a constant amount for any two characters. This could be explained if the factors were carried in a linear arrangement on the chromosomes; when crossing-over occurred at meiosis previously linked factors would be separated, and the chance of their being so should depend on the distance between them, for if the crossing-over can take place with equal ease

[1] The special case of the determination of sex and sex linkage, which is also important evidence, is referred to below (p 712).

at any point it is more likely to happen between two given points the farther they are apart. We can thus use the recombination values of different sets of factors to express their relative position on the chromosomes. Thus in another experiment with black vestigial fruit flies, in which another recessive character, purple eye, was also studied, Bridges found a recombination of 16.3 per cent. between *b* and *v*, of 6.4 per cent. between *b* and *p*, and of 10.8 per cent. between *p* and *v*. Since $6.4 + 10.8$ is approximately 16.3, we have support for the theory that the factors are linearly arranged, and that that for purple is situated about one-third of the way along from black to vestigial. The proof is almost perfect when it is found that hundreds of factors can be arranged in a consistent order on the chromosome. Such a plan is called a chromosome map. Many of the slight apparent anomalies in the recombination values can be satisfactorily explained in detailed ways which cannot be considered in an elementary book.

There are three other classes of evidence. There is sometimes an obvious connection between the number of chromosomes present and a variety of an animal—a characteristic form of the fruit-fly, for instance, has lost one of its fourth pair of chromosomes. In the salivary glands of insects the chromosomes are abnormally large, and it is sometimes possible to see structural changes in them which regularly correspond to known genetical characters or to variations in the linkage maps. Finally, in a few instances there is 'non-disjunction' of a pair of chromosomes in the formation of gametes, so that a germ cell contains two factors for each allelomorphic pair carried by the chromosome. This can be seen in the cells, and the heredity corresponds. These are the cases where the fundamental principle of Mendelism is untrue (p. 691). It should be noted that in this argument the genetical results have usually preceded the cytological observations, which have often been predicted long before they were confirmed. Mendel's work long antedated any knowledge of meiosis (or even, in any full sense, of fertilisation); the separate identity of chromosomes was postulated while cytologists still believed that they first appeared as a single thread or spireme; and crossing-over was predicted two decades before it was observed.

GENES

The factor situated on a chromosome—or perhaps making part of a chromosome—is now called a gene, and we must consider shortly what may be its nature. The simple Mendelian story which we have given so far is incomplete and in general incorrect in two respects. In the first place, the presence of a pair of genes does not necessarily lead to the production of the character to which they correspond : it will only appear if other conditions are right. In other words, there is at the nuclear as well as at the more obvious organismal level, a balance between heredity and environment. Height in man, for instance, is undoubtedly determined by a group of genes, but they can produce their full effect only when nutrition is adequate ; the recessive gene *cubitus interruptus* in the fruit-fly causes a break in one of the wing veins, but while at 19° C. all homozygotes are affected, at 25° C. half of them are normal. In these examples the genes are interacting with the external environment, but in others the interaction is with the internal environment of the animal's body. The colour of genetically dominant black rabbits can only be produced in parts of the skin to which a specific colour precursor, or chromogen, is supplied by the blood. If, as is probable, the presence of this chromogen is itself determined by a gene, we may speak of the final colour as being dependent on gene interaction. Secondly, instead of there being two alternative characters, there are often several possibilities, each being exclusive of all the others ; these (or their determiners) are known as multiple allelomorphs, and theory requires that only one factor from the whole set can occur in a gamete. A series of coat colours in the rabbit, ranging from natural or agouti to albino, is of this type, and another example is a series for reduction of the wings in the fruit-fly.

It is now possible to see some connection between the action of a gene and the control of protein synthesis by the nucleic aids described in Chapter 26. If a gene is a part of a chromosome—perhaps one of the loops on the bottle-brush—in which there is a particular pattern of bases in deoxyribonucleic acid, it will induce the formation of a corresponding molecule of ribonucleic acid. This in its turn will organise in the cytoplasm the formation of a particular protein. This will sometimes be an enzyme, which will mediate the carrying out of some process in the body.

It has long been apparent that some simple Mendelian characters are due to the failure of an enzymatic reaction ; the gene-product, for instance, that produces the black pigment in rabbits can be simulated by a peroxidase. More recently various hereditary defects in the blood of man have been shown to be caused by (or at least associated with) simple amino acid substitution in the hæmoglobin molecule. The simplest difference between a dominant gene and its recessive would be that the latter is simply the absence of the former ; the recessive homozygote would then have no opportunity to produce the enzyme or other protein on which the character depended, and the heterozygote might be expected to do so completely if one dose of the gene were enough, when there would be complete dominance, or only partially when the enzyme supply was inadequate and dominance would be incomplete. This explanation clearly cannot apply to multiple allelomorphs, where there are several possible states at one gene locus, and in fact there is evidence from *Drosophila* that very few recessive genes really do nothing. The gene scute–1, for example, reduces the number of bristles on the fly ; by the action of X-rays, which cause irregularities in meiosis, it is possible to get extra fragments of chromosomes in the sperms so that more than one gene of the allelomorphic series is present in a single nucleus. When two scute–1 genes are present the number of bristles is only a little less than normal ; with three it is greater than normal. The recessive gene must be able to carry out the reaction performed by the dominant, but less effectively. The simplest chemical explanation that can be given of the change is that there has been some minor alteration in the molecule of the protein. In sickle-cell anæmia, for example, where the amino acid glutamine in hæmoglobin is replaced by valine, oxygen can be carried, but not to the full normal extent. Other substitutions, such as an ethyl for a methyl group, are possible, and multiple allelomorphs would consist of a series of substitutions which left the basic nature of the gene unchanged. Similar changes are known to affect the activity of hormones.

The genes which we have been considering so far have been those which cause relatively large and obvious changes in the phenotype ; they are generally now called major genes. There are others, the polygenes, which individually are of very small effect, and can only be studied statistically ; there are usually a number having similar effects, so that they are replaceable

and a very complex series of genetic types is possible. Much continuous variation, as of size and weight, is due to environmental factors, but that part of it which is genetic in origin is probably always controlled by polygenic systems and is said to be multifactorial ; other polygenes are modifiers, producing small effects on the expression of major genes. Polygenes show segregation and linkage, although their effects are too small to be studied by the Mendelian method.

The effects of a gene are influenced not only by specific modifiers and variations in the environment, but by its position on the chromosome and by the sum total of all the other genes present. The position effect shows when by artificial means a gene is transferred from one part of a chromosome to another, the other when a gene is introduced by crossing into a new genic environment. The total pattern of genes, in which any individual gene is working, is called the gene complex.

DETERMINATION OF SEX

Most animals which have been carefully examined have an important cytological distinction between the sexes ; when the chromosomes are arranged in pairs at meiosis there is one pair which consists in one sex of two chromosomes which are not exactly alike. The odd one may be slightly different in shape, as in the vole (Fig. 29.8) where it is hooked, or it may be very much smaller, as in man ; in some species there may be a single chromosome left over with no fellow to pair with. It appears in fact as if one sex is cytologically heterozygous, and the normal inheritance of sex shows that this is so. In most animals, including mammals and flies, the males are heterozygous for sex, or heterogametic as it is called, but in birds and Lepidoptera the females are. The fully pairable sex chromosomes of the homogametic sex are called X, the odd one of the heterogametic sex is called Y. A cross between a female XX and a male XY should then give females XX and males XY in approximately equal numbers, and this is found to be generally true. Deviations from the fifty per cent. sex ratio can usually be explained in some other way, as for instance in mammals by a differential mortality in the uterus. It has been shown that the other chromosomes, or autosomes, have some influence in determining sex, but the main action is by the sex chromosomes.

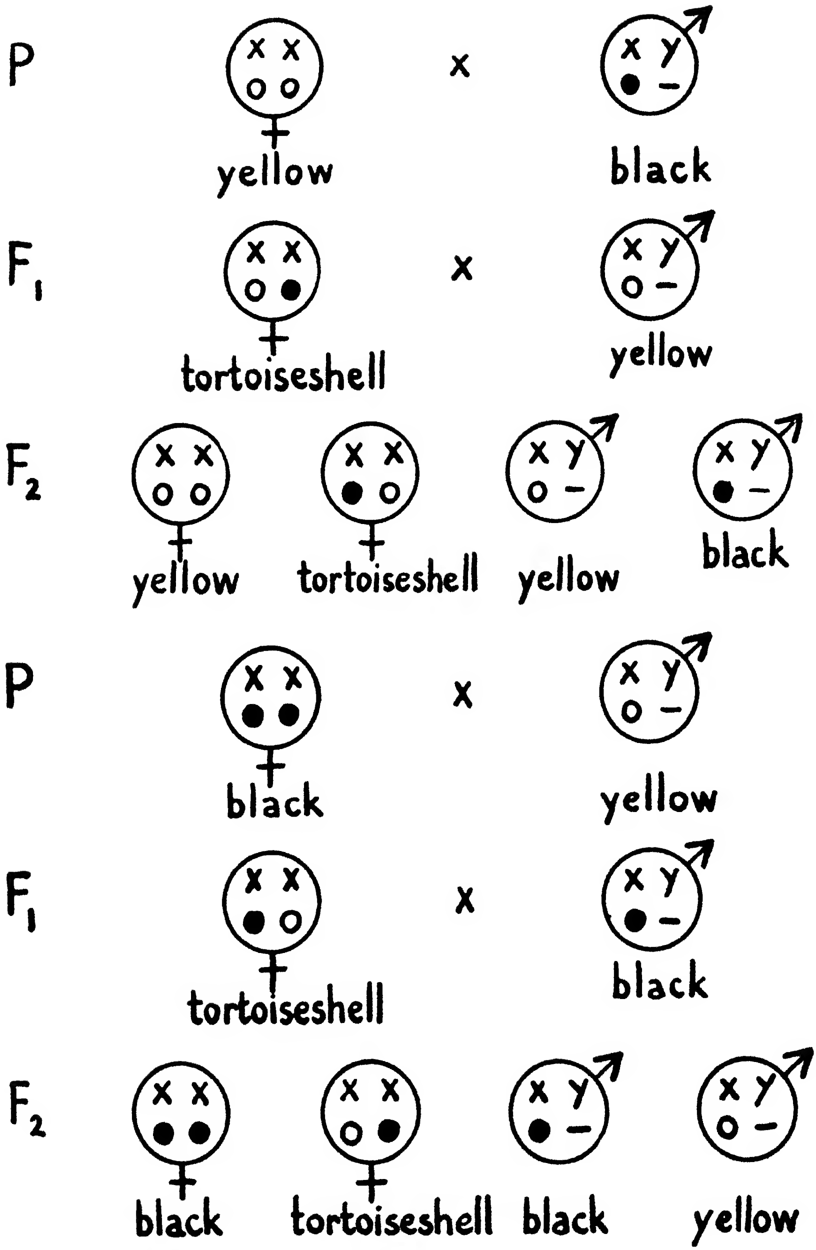


FIG. 29.12.—Crosses between black and yellow cats. O = gene for yellowness. ● = gene for blackness. — = absence of black/yellow gene.

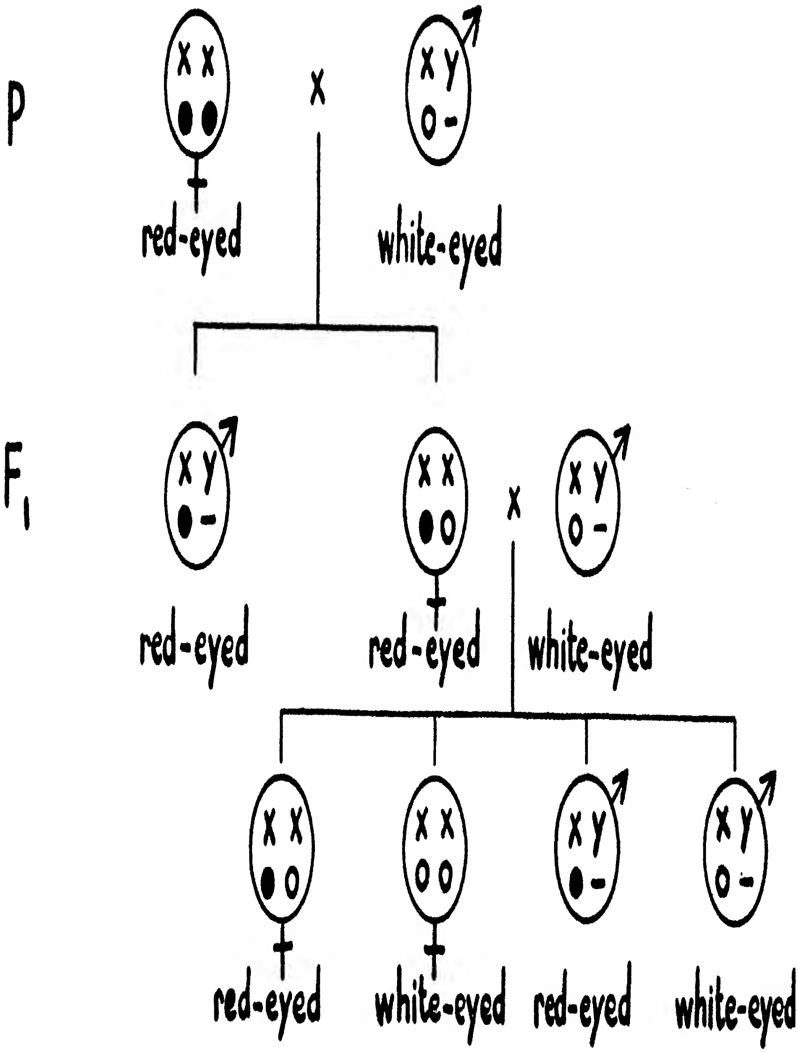


FIG. 29.13.—Sex-linkage in *Drosophila*.

●=gene for red eye; o=gene for white eye; — =absence of (red or white) gene.

SEX LINKAGE

If the sex chromosomes carry genes for any other characters one would expect their inheritance to be peculiar. In fact in many animals, as in *Drosophila*, the X chromosome carries a number of genes all of which are sex-linked. In the heterogametic sex they can never be homozygous, for they cannot exist in the Y. Fig. 29.12 shows the inheritance of the black/yellow colour difference in cats. The reciprocal crosses are different (this is a characteristic of sex-linked inheritance) and all the heterozygotes, which are tortoiseshell in colour, are females. (The very rare tortoiseshell males which are on record appear to be sterile abnormalities.) Fig. 29.13 shows the inheritance of eye-colour in *Drosophila*. Here red-eye (●) is dominant to white-eye (O). The cross between a wild-type homozygous red-eyed female and a white-eyed male will therefore give equal numbers of males and females, all red-eyed. But the females are heterozygous; bred with white-eyed males (i.e. back-crossed to the male parent) they produce all four possible types in equal numbers. Bred with a red-eyed male, the heterozygous females will give red-eyed and white-eyed males in equal numbers, but all the female offspring will be red-eyed, for although half of them will bear the white-eye gene from their mother, its effect will be overcome by the dominant red-eye gene which they must inherit from their father. Where a recessive sex-linked gene is rare, therefore, its effect will hardly ever be seen in the homogametic sex, for the character can only appear in this as the result of mating between two individuals carrying it, and the chances of such a union are small. This is the case for colour-blindness in man, which is inherited like white-eye colour in *Drosophila*, and is observed in only six females for every thousand males.

Sometimes the Y chromosome carries a gene which has no counterpart on the X; its effect will be apparent in the heterogametic sex only. An example is the normal allelomorph of barred feathers in chicks. The two X chromosomes of the male (the homogametic sex) cause a pattern which is visible on hatching; the female, which is necessarily heterozygous, has a different appearance, and so the chicks can be sexed without examination of their genitalia. In all these types of sex-linkage there can be no crossing-over between X and Y chromosomes, and this is confirmed cytologically. In some animals, e.g. gnats, parts of

the chromosomes do cross over, and genes situated here do not show complete sex-linkage. In most animals the Y is relatively empty, and contains very few genes.

CYTOPLASMIC INHERITANCE

For a long time it was generally assumed that all biological inheritance was Mendelian, and that the chromosomal genes were the sole determinants of development. There are strong theoretical objections to this view—it would seem to require that there should be no difference between the cytoplasms of different species of animals, which is absurd—and there is now increasing evidence that in plants and Protozoa there are also determinant particles or plasmagenes in the cytoplasm. One of the best known, called kappa, is associated with a nuclear gene K in *Paramecium* to produce the 'killer' property; individuals possessing this liberate into the water something which kills other 'sensitive' *Paramecia*. Both K and kappa must be present to produce killer, and both can persist unchanged for generations (K indefinitely, whatever the cytoplasm which surrounds it, but kappa only for four or five cell divisions in the absence of K), and then become active when they meet each other. Plasmagenes do not show Mendelian segregation, but they do show dilution; that is, their effects bear some relation to the amount of cytoplasm which is inherited. They are self-propagating, and in normal circumstances their multiplication keeps pace with that of the cell. Sometimes, as by an increased food supply to *Paramecium*, the cell may be made to divide more rapidly than the plasmagenes; kappa has by these means been made so dilute (that is, there are so few particles in the cell) that it has no effect, but by a slowing down of the rate of cell division it was enabled to catch up and become active again.

Further evidence for the importance of the cytoplasm has come from the transfer of nuclei from one species or strain of *Amœba* to another. When this experiment is carefully carried out, the mixed animal survives and reproduces, and the members of the clone descended from it are intermediate between the two parents in many measurable characters and the changes have been stable over eight years. The cytoplasm in fact seems to have rather more influence than the nucleus (Fig. 29.14). Its effects are perhaps produced by plasmagenes, which may be thought of as

points where nucleic acid is replicated, or perhaps by the supply of coenzymes produced in some other way.

There is no reason to think that the Metazoa are different. *Dauermodificationen*, changes produced in *Drosophila* by high temperatures, and inherited, but for a few generations only, are perhaps best explained by changes in the cytoplasm.

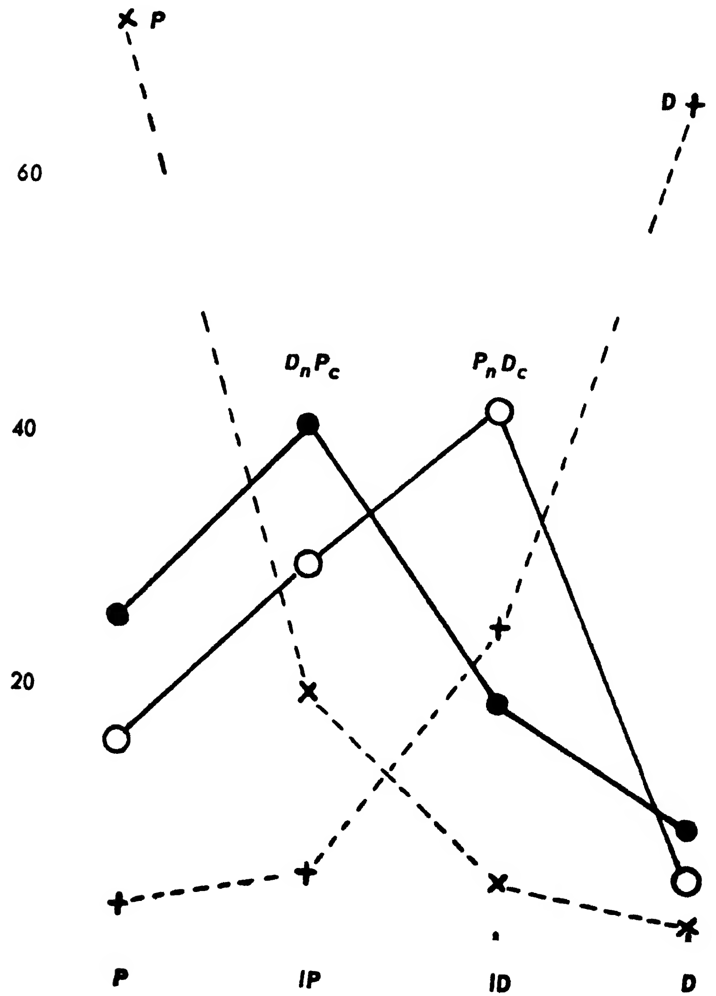


FIG. 29.14.—The shapes of *Amœba*.

Abscissæ—shapes: P = typical *proteus*; D = typical *discoides*; IP = intermediate, but more like *proteus* ID = intermediate, but more like *discoides*.
Ordinates—numbers of individuals: P = *proteus*; D = *discoides*; D_nP_c = *discoides* nucleus in *proteus* cytoplasm; P_nD_c = *proteus* nucleus in *discoides* cytoplasm.—From Danielli, *Ann. N.Y. Acad. Sci.*, 1959, 78, 675.

30

THE ORIGIN OF SPECIES

CLASSIFICATION

FROM the earliest times, as shown by the Mosaic story, thinking man has recognised the existence of different sorts of animals and has felt the necessity of giving them names. It is these nameable sorts which the zoologist now calls species; at an elementary level there is no difficulty about what we mean by the term, for cats are clearly distinct from dogs, and no one expects cats to produce puppies or dogs to produce kittens. Cats are even clearly distinct from tigers, although there is so much similarity between them that the description 'big cat' applied to a tiger seems natural and obvious. When animals are more widely studied difficulties appear. There are obviously several different sorts of cat: tame cats and wild cats, tabby cats and ginger cats, Manx cats and tailed cats, and the number of species of cat, whether one or two or many, becomes a matter of opinion. No satisfactory definition of 'species' has ever been produced, and for that reason experience in the study of the animals concerned is very important; hence it has been said that a species is that which is considered as such by a competent authority. This is a half-truth, but more important is the fact that even authority must work to some rules. All the members of one species must have most of their features in common; these features must be consistently transmitted from parent to offspring, or at least to their remoter issue; and, if there is sexual reproduction, two individuals of the same species and of opposite sex should be capable of fertile union. It is on the last point that disagreement is least likely to be resolved, for a decision must often be made without the possibility of putting the matter to experimental proof. No one, for example, has ever tried to find out if all the possibly conspecific birds living in Spain and China will interbreed, but meanwhile a working decision about their specific status must be made. Moreover, the breeding criterion does not work in reverse, for there are plenty of examples of interbreeding in captivity between animals which no one regards as anything but different species; species hybrids between a number of different pheasants, for instance, are completely fertile. The criterion that we are

looking for is absence of *natural* interbreeding, and this, unfortunately, we can only get if the two supposed species live alongside each other.

When the systematist has determined a species he gives it a specific name. This is in Latin, and consists of a noun, written invariably with a capital initial letter, qualified by an adjective, written with a lower-case initial ; the whole is normally printed in italic. In addition to following the ordinary rules of accidence, the names, where they are derived from non-Latin words, should conform to certain rules of transliteration, which, like the other conventions about these names, have been agreed by the International Zoological Congresses. It sometimes happens that two or more people give different names to the same species ; the one which takes precedence is then the earliest to which an adequate description, in words or drawing, is attached, but no names are recognised which are earlier than the tenth edition of Linnæus's *Systema Naturæ* (1758). There is, however, a growing feeling in favour of *nominanda conservanda* which will not be changed even if precedent names are dug out of the literature. The object of Latin names is to ensure precision and international understanding, but in many groups they have been changed so much and so often that in referring to old books one has to go by the vernacular names in order to know which species the author is talking about.

The noun part of the specific name is shared by a group of species which have considerable similarity. It is called the generic name, and species to which the same generic name is given are said to be of the same genus. The adjective by which each species is distinguished is called its trivial name.[1] Thus the wild cat of Europe is of the genus *Felis*, and is distinguished by the trivial name *silvestris* ; the species is *Felis silvestris*. Other cats are *Felis ocreata*, the Egyptian cat, and *Felis tigris*, the tiger. When there can be no confusion the generic name may be abbreviated to its initial letter. It often happens that with increase of knowledge it becomes necessary, or with the discovery of more species it becomes expedient, to split a pre-existing genus into two or more. Thus Linnæus used the generic name *Motacilla* for a wide range of soft-billed birds, including wagtails, warblers, nightingales,

[1] It is also sometimes called the specific name, but as the species is only defined if the generic name is used (or made clear from the context) as well, this is a misleading usage.

and the redbreast. These are now separated into half a dozen genera, and *Motacilla* is used only for the wagtails. This may necessitate the change of an animal's generic name without a change in the trivial. A name so altered is shown by following it with the name of the author responsible for the trivial name enclosed in brackets. An author's name (or a standard abbreviation of it) without brackets shows that the whole specific name was given by him. For example, the redbreast is *Erithacus rubecula* (L.), because Linnæus used the trivial *rubecula*, but the generic *Motacilla*; while the pied wagtail is *Motacilla alba* L.

In much-studied groups of organisms, especially birds and some orders of insects, it is convenient to recognise groups within the species, and these, called subspecies, are distinguished by trinomials, a second adjective being added to the specific name. For example, the pied wagtail of Great Britain is *Motacilla alba yarelli*, while the Continental form, the white wagtail, is *Motacilla alba alba*. The system of application of authors' names to trinomials is in confusion, but fortunately they are of no importance to the elementary student.

The further process of classification consists in arranging the genera into series of groups, each containing more and more species which have less and less in common. The chief categories, in ascending order from the genus, are families, orders, classes, and phyla, but other categories, such as sub-families and super-orders, are often interpolated to make it easier to manipulate large numbers of species. All these groups have Latin names, which are plural nouns. Family names are derived from generic names by the addition of *-idæ* to the root, for example Felidæ, the cats, and Motacillidæ, the wagtails and pipits, but there is no rule for the others. Group names are not italicised. Anticipating what comes below, we may add that it is now customary in classifying animals to attempt to show not only the features which they have in common with each other, but also the genetic relationships which they may be supposed to have according to the hypothesis of organic evolution.

The existence of species poses the problem of their origin, and, to solve this, three main hypotheses have been proposed. The first, that species have always existed as they are now without beginning, has been held by few educated people, and all that we know of the history of the earth is against it. It has been attributed to Aristotle and to Duns Scotus (1265 ?–1308)

but need not be considered further here. The second supposes that at some point or points in time species have been created by an immaterial god. The commonest form of the hypothesis, known as special creation, supposes that existing *species*, as we now know them, were created more or less together, and that since then there has been no change beyond the limits of the species. This is illustrated by the biblical story of the creation, but its development as a scientific hypothesis came after the reformation and is mainly the work of the eighteenth century. Another form of the hypothesis, known as catastrophism, was developed by Cuvier (1769–1832) to account for the fossils of extinct animals found in the rocks. It supposes that there have been several creations, followed by complete or partial cataclysms, leading to widespread extinction of forms.

EVOLUTION

Theories of creation are only possible to theists, and no atheist before the nineteenth century seems to have had any clear idea of what he would have put in their place. Some eighteenth-century writers, such as Buffon (1707–88) and Erasmus Darwin (1731–1802) had hazy ideas that one species might be derived from another, but it was not until the nineteenth century that the third hypothesis, that of organic evolution, became of any importance. It postulates that all existing species are derived by descent from other species, which are in general simpler in structure. Its development was largely due to the writings of Alfred Russell Wallace (1823–1913) and Charles Robert Darwin (1809–82) who in 1858 contributed simultaneous papers to the Linnean Society in which they put forward the view that species had evolved by a process of natural selection of those races most fitted to survive in particular surroundings. Darwin's *Origin of Species* followed in 1859. It is often said that the strength of argument and wealth of illustration which Darwin employed compelled belief in organic evolution. This is in part true, but at least as important is the time at which he wrote. As Lecky says of the history of religious thought, the success of any opinion depends 'much less upon the force of its arguments, or upon the ability of its advocates, than upon the predisposition of society to receive it'. Darwin lived at a time when there was increasing distaste among the intellectual public for believing in divine interference in the affairs of the world. Evolution is

not, as Darwin himself recognised, incompatible with creation, but it puts the necessity for creation further back in time and reduces the number of creative acts which are necessary. It therefore enables men to forget the origins of things in directing their attention to more recent happenings. We must now consider the sort of evidence which convinced people that evolution was a reasonable hypothesis, and then the mechanism by which it may be supposed to have come about.

1. The only direct evidence for evolution would be to see it in action. There can be little doubt that new species of plant have arisen in historic times, but we have no similar evidence

FIG. 30.1.—*Amphidasis betularia*. A normal female below, a melanic female above.—After Lemche.

for animals. We do know, however, instances where the form of a species has changed. The normal form of the peppered moth, *Biston* (=*Amphidasis*) *betularia* (Fig. 30.1), has mottled wings, but in 1850 a dark and uniformly coloured variety, later called *carbonaria*, was discovered in Manchester. This melanic type spread, slowly at first, until by 1910 it was, in the industrial north, present in equal numbers with the normal form. By 1950 there were hardly any of the normal form in the industrial north, while in the rest of England *carbonaria* was spreading more slowly. The dark type might be considered as a subspecies, and it is not unreasonable to think of subspecies as incipient species.

2. Parallel with a few observations which have been made in nature on the change of form of animals are the many on the changes which occur under domestication. The actual origin of most of our domestic animals goes back to the obscurity of

prehistory, and perhaps often involves hybridisation which would not occur in nature, but there can be no doubt that within historic times changes have been produced simply by selection. The peculiar appearance of the dogs and cattle in seventeenth- and eighteenth-century pictures cannot be ascribed to the poor

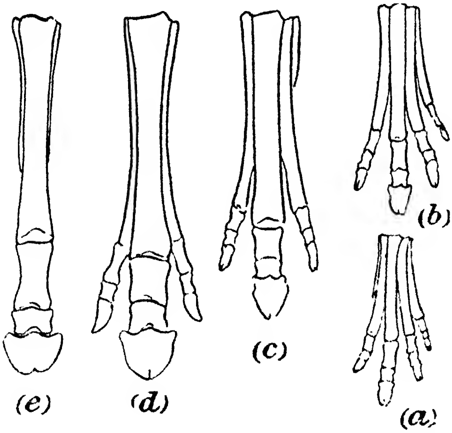


FIG. 30.2.—The bones of the forefoot of a horse compared with those of earlier members of its family.—From Swinnerton.

(*a*) *Eohippus* (*Hyracotherium*) (Lower Eocene); (*b*) *Orohippus* (Middle Eocene); (*c*) *Mesohippus* (Lower Oligocene); (*d*) *Hypohippus* (Lower Pliocene); (*e*) *Equus* (Upper Pliocene to present).

draughtsmanship of the artists, for the men and women in them differ only in clothes from those of the present day. We know that in cattle there has been conscious selection for certain valuable qualities of beef and milk yield, and also for certain colour types such as the red-bodied white-faced Herefords, and there has probably been unconscious selection in other directions as well. This selection has changed the type, and it was a great part of Darwin's argument that what man could do in a short time nature could do in unlimited centuries.

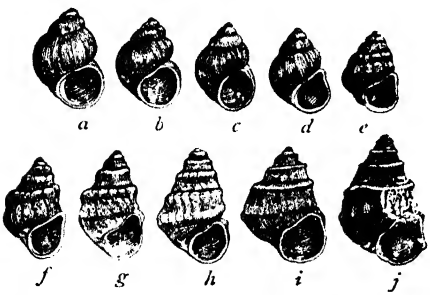


FIG. 30.3.—The gradual transition between *Paludina neumayri* (*a*) the oldest form, and *Paludina hœrnesi* From Neumayr.

3. In Darwin's time palæontology, the study of fossils, was little developed, but he realised that, if evolution had occurred,

the rocks should provide a record of it in gradually changing species from the older layers to the newer. To some extent his prediction has been fulfilled; we can trace a gradual increase in size of the horses, and a progressive reduction in the number of their toes (Fig. 30.2). In the elephants we can see the increase of tusks and trunk, and reduction of molar teeth. In various groups of molluscs, echinoderms and other invertebrates with an exoskeleton we can trace changes in the shape, size, and markings of the shell (Fig. 30.3). Where the different types are found in successive layers of the same rocks in the same place there can be no reasonable doubt that those at the lower levels were the ancestors of those above, and that specific and generic changes have occurred. On a wider scale there is a danger of arguing in a circle. The rocks all over the earth are arranged in a succession to which a rough time-scale can be given (Table XII), but correlation between one part of the world and another is largely

TABLE XII.

Era	Period	Duration, in million years	Millions of years since beginning	First appearance
Quaternary	Pleistocene	1	1	Man
Cœnozoic or Tertiary	Pliocene	11	12	
	Miocene	16	28	
	Oligocene	11	39	
	Eocene	19	58	
	Palæocene	17	75	
Mesozoic or Secondary	Cretaceous	60	135	Placental Mammals
	Jurassic	45	180	Birds
	Triassic	45	225	Mammals
Palæozoic or Primary	Permian	45	270	Therapsids
	Carboniferous	80	350	Reptiles
	Devonian	50	400	Amphibians, Teleosts, Insects
	Silurian	40	440	Fish
	Ordovician	60	500	Vertebrates, Eurypterids, Arachnids
	Cambrian	100	600	Trilobites
	Precambrian	2100	2700	

made on the occurrence in different rocks of similar fossils. Changes in the two sets of fossils cannot subsequently be legitimately used as evidence for evolution, although they may be built up into a story which is not incompatible with it.

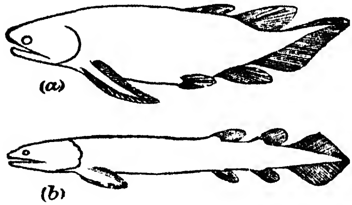


FIG. 30.4.—Extinct crossopterygian fishes.—From Swinnerton.

(a) *Notoptychius*; (b) *Glyptopomus*. Note the stout central portions of the fins, containing skeleton and doubtless muscle, and thus having the makings of legs.

In addition to the relatively small number of lineages which have been worked out, there is general evidence that the simpler or structurally less advanced groups appeared earlier than the more complex ones. Fish occurred before Amphibia, these before reptiles, and reptiles before birds and mammals. Occasionally 'missing links' are found, isolated fossils which partake of the nature of two groups and stand between them in time. *Archæopteryx*, for example, of the Jurassic, was a bird-like animal with

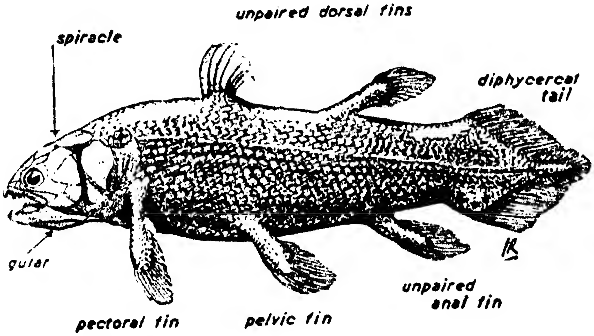


FIG. 30.5.—A living crossopterygian, *Latimeria chalumnæ*.—From Thorne.

Drawn after a photograph by J. L. B. Smith. $\frac{1}{20}$ natural size.

teeth and a reptilian tail (Fig. 23.24). *Tritylodon*, a small creature from the Triassic, was formerly regarded as the earliest of true mammals, but is now considered to be a reptile on account of its jaw articulation; it may reasonably be considered to be something between the two, and without a knowledge of its whole structure and mode of life, which we are never likely to have, it does not much matter which we call it. Within the phyla, then, palæontology strongly suggests evolution. For the origins of the phyla, it gives no evidence one way or the other.

4. The distribution of animals includes another group of facts of which Darwin made much in his argument for the probability of evolution. The origin of the distribution of animals, like all other distributional problems, may be divided, in modern terms, into the geographical and ecological aspects, the former paying attention to mere distance as an isolating factor, the latter to special qualities of the environment. It is obvious to any traveller that on the whole the farther apart two places are, the less similar are their faunas. This could be explained by several creations in different places, with some limited subsequent movement and mixing, but it is equally well explained by a single origin of each ancestor, followed by movement and evolution in different parts. The regular occurrence on islands of animals similar to, but specifically distinct from, those of the nearest mainland, coupled with the fact that the greater the distance between island and mainland the greater the difference in their faunas, strongly suggests descent with modification—a common ancestor for each related pair of species on island and mainland, followed by independent evolution. The Galapagos Archipelago, situated on the equator over five hundred miles from Ecuador, has a fauna which is characteristically American in type, although most of the species are found only in the islands. The Canary Islands, only a hundred miles from Morocco, have a North African-European fauna, with far fewer species of their own. In both groups of islands there are some species, and more subspecies, confined to a single island. Subspeciation is shown in Great Britain, for example in the birds. Although it is doubtful if any of our birds are specifically distinct from those of the Continent of Europe, many are of recognisably distinct subspecies, and the wren, a very sedentary bird, although our mainland form is not distinguishable from that of the Continent, has subspecies *Troglodytes troglodytes hirtensis*, *T. t. zetlandicus*, and *T. t. hebridensis*, on St. Kilda, Shetland, and the Outer Hebrides respectively. Other subspecies are found in the Faroes, Iceland, Corsica, and Cyprus.

The faunas of similar environments in different parts of the world may be superficially similar, but they always show differences corresponding to the differences between other animals living in the same geographical region. This is well shown wherever there are ecological islands, as, for example, the tops of high mountains. The Andes have an alpine fauna, but it is American ; that of the Swiss Alps is European. Caves show the

same thing even more strikingly. Those of Carniola in Yugoslavia and Kentucky in the United States are both in limestone, and the animals in them—urodeles, fishes and invertebrates—are very similar, with characteristic modifications such as blindness, but their structural affinities are with the animals of the continent in which they are situated.

5. The student who has read as far as this chapter will have realised that a comparative treatment of morphology is only possible because to a great extent different animals are built on the same plan. We can recognise the cell in almost all animals and most plants. The nephridium, a hollow ingrowth from the exterior ending in a tuft of cilia, can be seen in Platyhelminthes, Annelida, Rotifera, Mollusca, and *Branchiostoma*. The general plan of the vertebrate skeleton is similar throughout the group, and within a class there may be only small differences in shape in the bones of corresponding positions (Fig. 30.6). Many animals contain apparently functionless vestigial organs, such as the appendix and dermal muscles of man, which seem to represent structures which in other animals, such as the rabbit and horse in the examples given, have physiological value (Fig. 30.7). None of this by itself constitutes evidence for organic evolution, for there is equally a comparative morphology of things like motor cars which also may contain vestigial structures, although the theory is inapplicable to inanimate things ; but taken together with the fact that, so far as we know, new individual animals only arise by reproduction from pre-existing animals, whereas each new motor car is made *de novo*, it does.

6. Similarly, comparative physiology supports the theory of evolution, in that the general pattern of nucleic acids and enzyme systems extends almost throughout the living world, and in general the closer the structural relationship between two animals the greater is the resemblance between the chemical processes that go on within them.

7. Even when the adults of two species of animal resemble each other very little, their embryos may do so much more strongly. This, sometimes known as Von Baer's Law, or the biogenetic law, was known as a generalisation some years before the theory of evolution was established. As evidence for that theory, it is really an extension of that from comparative anatomy. As we have seen above (p. 671) early stages of chick and rabbit are almost indistinguishable ; this means that their structural

plan is then the same, although as they grow they become progressively less like each other. Similarly, adult polychætes

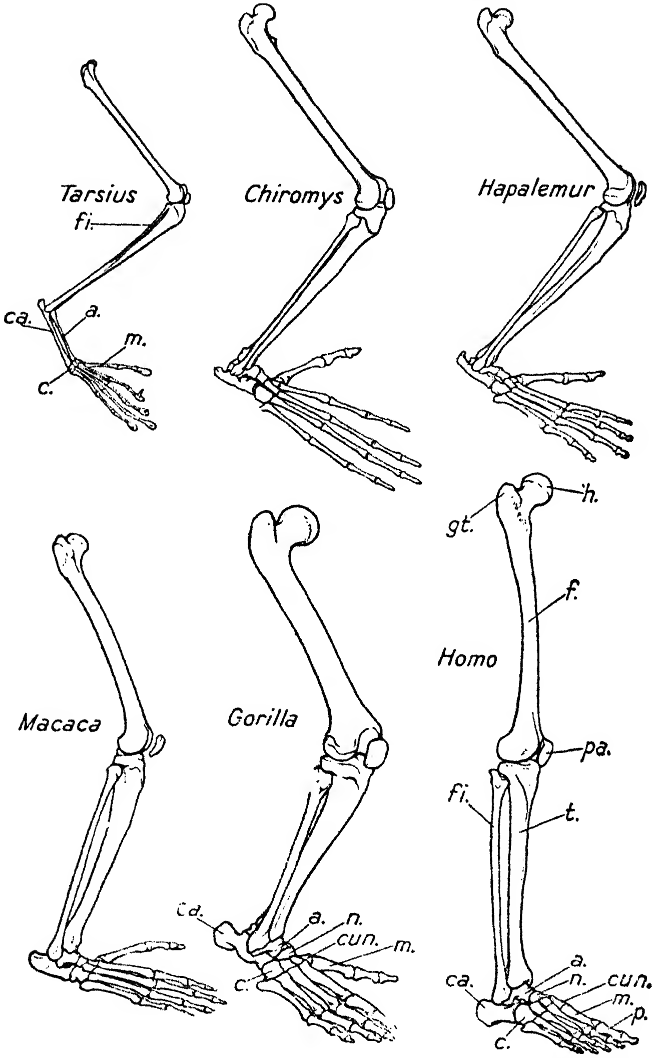


FIG. 30.6.—Bones of the hind leg and foot of primates (not to the same scale).—From Young, *The Life of Vertebrates*, 1950. Clarendon Press, Oxford.

a., Tibiale ; *c.*, unciform ; *ca.*, fibulare ; *cun.*, mesocuneiform ; *f.*, femur ; *fi.*, fibula ; *gt.*, greater trochanter ; *h.*, head ; *m.*, first metatarsal ; *n.*, navicular ; *p.*, proximal phalanx ; *pa.*, patella ; *t.*, tibia.

and molluscs have not much resemblance, but the trochophore larva is common to both (p. 679), and earlier still the spiral cleavage of the egg is almost identical in the two groups. We

may sometimes then be able to find relationships in the embryos which are not apparent in the adults ; the sessile barnacles, and even more such parasites as *Sacculina* (p. 235), are hardly recognisable as Arthropods, but their larvæ are clearly Crustacea. The form in which the biogenetic law is sometimes stated, that ontogeny recapitulates phylogeny, or that in the course of its

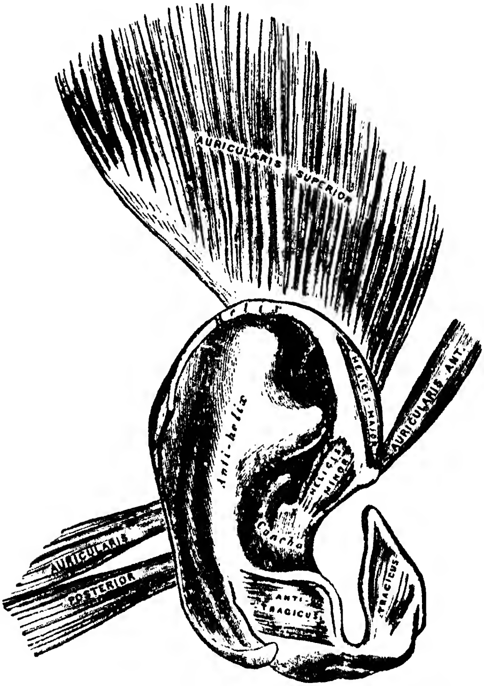


FIG. 30.7.—A dissection of the human ear to show the useless vestigial muscles.—From Gray.

life an animal climbs up its family tree, cannot be maintained, but embryology does bring to light many transient vestigial structures, such as the gill slits of terrestrial vertebrates.

8. What is generally called the evidence from classification is also an extension of that from comparative anatomy, as the fact that animals can be classified at all depends on their similarity of structure. The difficulty of deciding on the limits of many species suggests that there are no real limits ; the less common difficulty of deciding on the limits of an order or a class, as with *Tritylodon* mentioned above (p. 722), points to the same conclusion. Perhaps more important is the fact that classifications based on

superficial examination are often contradicted by a knowledge of internal structure. Whales, for instance, were for long regarded as fishes, but dissection shows them to be mammals ; even more obviously, bats are not birds, as their wing skeleton is different and easily derived from that of mammals (Fig. 30.8). The theory of evolution has, however, had more influence on classification

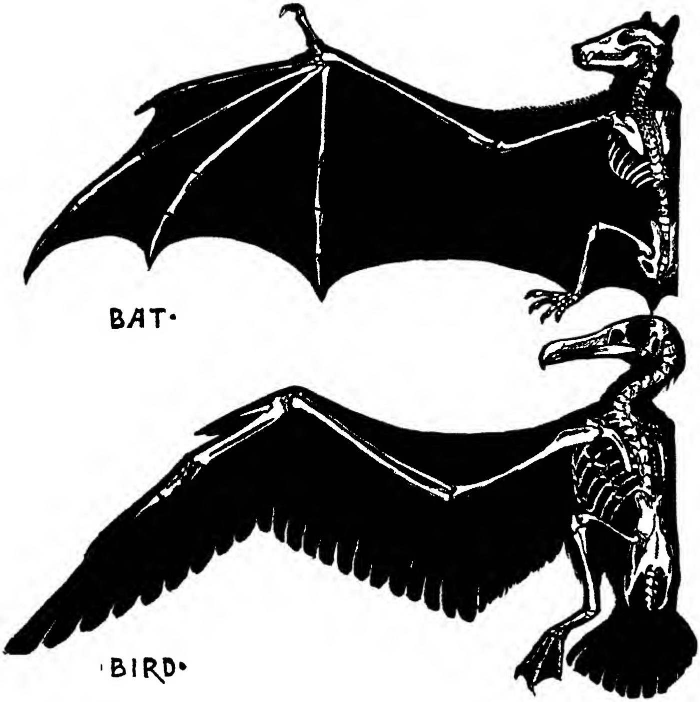


FIG. 30.8.—Diagrams to show the difference in construction between the wing of a bat and that of a bird. In the bat all the digits are present, four of them are very long, and the wing surface is provided by skin stretched from finger to finger and between the arm and the flank. In the bird there are only three digits, these are vestigial, and the wing surface is mainly provided by feathers in rows parallel with the axis of the limb.—From Romanes.

than has classification on evolution, since most taxonomists now attempt to make their systems show not only similarity in structure but also community of descent. This is, however, not always possible and is always of necessity conjectural, so that fundamentally classification remains a matter of associating like things.

NATURAL SELECTION

Organic evolution could not become an important hypothesis to account for the origin of species until some means was suggested by which it could be reasonably supposed to have taken place. Such a means was first convincingly argued by Darwin and Wallace. Their theory of natural selection, or the survival of the fittest, appeared to be logical, and indeed, on the facts as they knew them, inevitable. It started from the observation, first demonstrated for human populations by Malthus in 1802, that many more offspring are produced than can possibly survive. This is most obvious for animals like fish or parasites which lay millions of eggs in a year, but is also true of mammals and birds, where each pair on an average produces more than two offspring, yet the total numbers do not increase. To this observation was added the phenomenon of variation—the fact that no two individuals are ever quite alike—and the deduction that, of a group, those most fitted to live in a particular environment would survive rather than those less fitted. 'Survival' is here a relative term; what matters is the number of descendants which the individual leaves, and the argument is that the better an animal is suited to its environment, the longer it is likely to live and the more descendants it is likely to leave. The theory was completed by adding a third observed generalisation—that like begets like—and a usually concealed assumption that while the range of variation would remain roughly the same, the mid-point would gradually shift in the direction of the selection. If one considers, for example, a carnivorous mammal feeding on mice, it is obvious (that is, we assume) that the most agile individuals will catch the most mice, and so be most successful, especially in times of famine or when there are barely enough mice to go round. They will therefore leave more descendants, and by inheritance these will be more agile than the average, not only in that none of them will be very sluggish, but also in that some of them will be more agile than their parents. This will go on generation after generation, and eventually the animals that we call cats will be produced. At the same time selection will also have operated on the mice, choosing those best able to escape from the cats by speed, secretiveness or cunning.

Neither nineteenth-century biologists, nor those who opposed the theory of evolution on religious grounds, saw the real weakness

of the Darwinian theory, which is the assumption that with selection would go a progressive change in the limits of variation. No evidence for this was given, and even if it had been, a complete theory would still have needed to find some explanation of how it was brought about; we shall return to this last point later. In fact we now know that in the form in which Darwin made it, the assumption is untrue. Much 'continuous variation', on which alone he based his theory, we now know to be not inherited at all; it is phenotypic only, and caused by environmental influences in each generation. That part of continuous variation which is genotypic (and largely caused by numerous genes of small effect, or polygenes) could only be selected until the genes were all homozygous; beyond that point selection could produce no further change.

In spite of these difficulties, the modern theory of evolution is based on natural selection, but it also takes account, as Darwin was unable to do, of Mendelian and post-Mendelian genetics. Selection within a species is assumed to take the existing genotypes as far as they can go, not only in favouring individuals which are homozygous for valuable characters, but in fitting particular genes into a set of other genes in the presence of which they can exert their maximum effect; in selecting, that is, a favourable genotype. If success in this direction has been already achieved by any given species in its natural environment, the further role of selection will be largely conservative; it will maintain the type, and only when the environment changes, as with the melanic moths in industrial England described above (p. 719), will it work instead so as to change the type.

MUTATION

The action of selection would be different if new genotypes arose, for these would be in competition with the old, and selection would determine which survived or, if both survived, in what proportion. In all the species which have been intensively studied, there is evidence that new genotypes, or mutants as they are called, do occasionally arise. The mutations, or nuclear changes which produce the mutants, are of three main types. Numerical mutations are changes in the numbers of chromosomes, and structural mutations are changes in the arrangement of the genes on a chromosome. They clearly add nothing new, but may have considerable effects

on the expression of a given gene. They might account for some subspeciation or speciation, but not for any evolution on a wider scale. Gene mutations are changes in the nature and so in the effect of a gene. The rate at which they occur varies, but is seldom much more than of the order of 1 in 10^6 meioses. They allow much wider scope for evolution, for we know that the different allelomorphs of a gene may have widely different effects, and if all the genes in any animal mutated together the effect would be large.

ISOLATION

We now know a good deal, from the theoretical point of view, of the possible effects of selection in changing the genotype, that is to say, we have mathematical formulæ which connect rate of spread of a gene with its mutation rate and its selective advantage. Unfortunately we know very little about the magnitude of mutation rates in nature and even less about the selective advantage which any naturally occurring gene may confer, so that from the practical point of view the mathematics tells us chiefly what we knew before—that if mutation rate and selection rate are large enough evolution will occur. It has, however, brought out two important points which were not previously fully appreciated. The most important is that, at any rates of mutation and selection which are likely, evolution in the sense of splitting of one species into two, will only occur if there is some degree of isolation of the two evolving populations. The frequency of endemic species or subspecies on islands is thus explained, for here there is often complete or nearly complete isolation from the population of the mainland. Mere distance may also be important, for an animal living in Spain has no chance of breeding with one living in China. It is not surprising therefore that over a large land mass such as Eurasia there are many examples of series of subspecies or congeneric species replacing each other in turn. The nuthatch (*Sitta*), for instance, has a dozen or more forms, variously described as species or subspecies, ranging from Japan to the Canaries (and there are others in America) and differing chiefly in size and in whether the breast is white, buff, or grey. This bird also illustrates a point which is fairly general—that the Japanese and West European forms resemble each other more than they do those of the intervening continent. Where separate forms cannot be recognised

there is often a cline, that is, a gradual change either in the magnitude of some measurable character, such as size, or in the frequency of occurrence of a particular character. An example of the second type is given by the change in the percentage of the bridled form (Fig. 30.9) of the guillemot (*Uria aalge*) present in the breeding colonies as one goes from south to north. This type, which has a white line running back from the eye, is not present in Portugal, makes about 1 per cent. of the birds in the

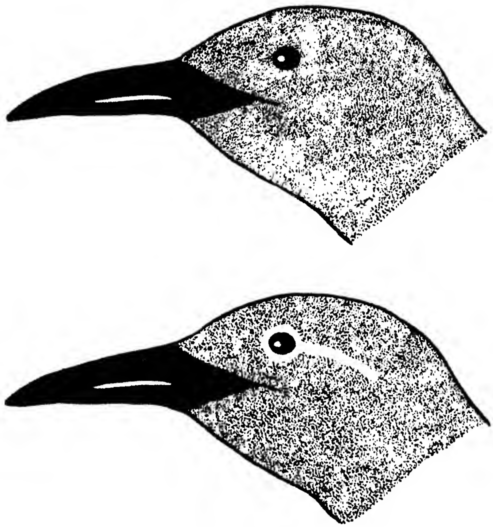


FIG. 30.9.—Heads of bridled guillemot (below) and of the normal variety (above).

English and Bristol Channels, and then becomes fairly steadily commoner until there are from 10 to 16 per cent. round the north coast of Scotland and in the Hebrides. Farther north still it becomes even more important, and makes over 50 per cent. of the birds in Iceland (Fig. 30.10).

Many species of animal are probably so sedentary in habits that the effective choice of breeding partner is small. A number of populations of Lepidoptera, which are known to be isolated have been shown to change with time in a small but measurable character, such as the number of spots on the wings of the meadow brown, *Maniola jurtina*, and in some cases the change can be correlated with a physical factor such as drought. On the other hand, wide-ranging active animals, such as many mammals, birds and fish, and small species which have resting eggs or other

distributive stages which can be blown by the wind or carried in other ways, for instance on the feet of birds, have very little isolation. The melanic moths which have evolved in the past century must have been more or less sedentary ; if, however, the

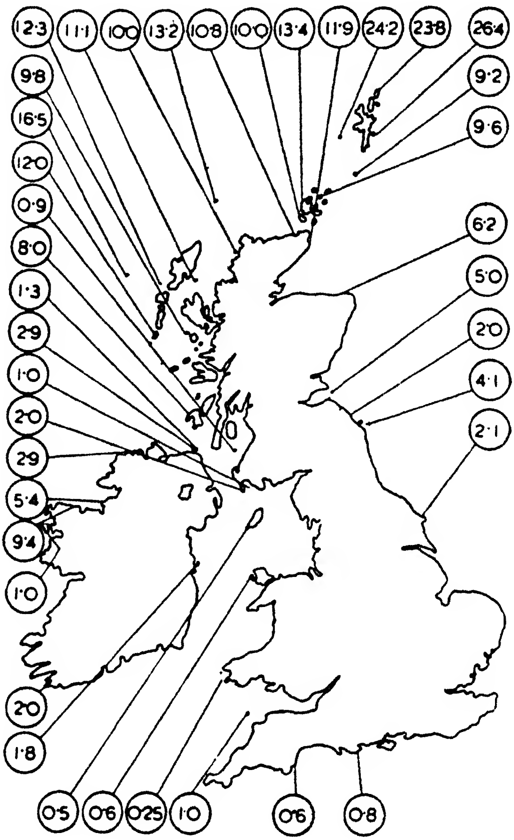


FIG. 30.10.—Map of the British Isles showing the percentages of the bridled form of the guillemot at breeding colonies in 1936–41.—From Southern and Reeve, *Proc. zool. Soc. Lond.*, Series A, 1941, 111, 264.

change in environment had occurred over the whole range of the species the transformation could have taken place without isolation. In this way one species may change into another, but cannot split into two.

Besides the various types of geographical isolation, such as by water, deserts, mountains and mere distance, it is probable that other types may have been important in speciation. Many

insects have races with different food plants, which makes ecological or habitat isolation. Parasites with different hosts are similarly separated, and it is possible that habitat preferences, reinforced by a homing instinct, are important in fishes, birds and mammals, although many ornithologists would deny this. Seasonal isolation is possible, where different mutants become sexually active at different times of the year, and in species with copulatory organs a single mutation could produce structural isolation. In the higher animals there may be psychological or behavioural isolation—refusal to mate with an individual who does not show the characteristic recognition marks or precoitional behaviour of the species. All these may lead to subspeciation and then to a genetic isolation or incompatibility ; at this point or before the one species has become two.

DRIFT

The second discovery of the mathematicians is that both the rate and the type of evolution depend on the size of the breeding population or deme. Evolution will be most rapid when this is moderate. When it is small (perhaps less than about 1,000) selection becomes less important, and may be entirely overcome by drift, a random spread of genes depending on the chance of their mutation and survival. Not everyone is agreed on the importance of drift, but if it does occur it would account for the apparently useless quality of many specific characters.

POLYPLOIDY AND HYBRIDISATION

The chromosome numbers of many related species of plant run in series which are multiples of a basic number, which strongly suggests that the species with the higher numbers have arisen by polyploidy, the multiplication of complete sets of chromosomes in one germ cell. Stable hybrids would then become possible, leading to further new species. The chromosomes of animals are much less well known, but some series suggesting polyploidy have been reported in annelids and other groups.

SUMMARY

We have then a modern theory of natural selection, which depends on mutation, isolation and selection ; to these some

writers would add drift. It sometimes escapes notice that this leaves the most important part of evolution, the origin of mutation, without explanation, and here we are little better off than was Darwin. We know, as he did not, that the evolutionarily important part of variation is produced by changes in the genes, but we can go little further. It is a reasonable guess, as we have seen above (p. 708), that a mutation involves a change in the chemical nature of the gene, but so far as our evidence goes such changes seem to take place by chance; that is, we can find no reason why the change should take place at one meiosis rather than another. We can increase the rate at which mutation occurs, that is, the proportion of genes which change in a large number of meioses, by such agents as X-radiation, high temperature and chemicals, but in this we do nothing new; we merely increase the existing instability of the nucleus. Even if we did know of a mechanism by which we could cause genes to mutate in a particular direction, we should still know little about evolution above the species level, for here we need an explanation of the origin of new genes. We know of a group of genes which produce wings, absence of wings, small wings, and various types of abnormal wings in *Drosophila*, but for a complete theory of evolution we need to be able to suggest a mode of origin of these genes in the primitive wingless arthropod ancestor from which we assume *Drosophila* to be descended.

Some of the earlier writers on evolution saw this difficulty more clearly than do many of their successors. Buffon supposed that the direct effect which the environment undoubtedly often has on an organism, for instance the tanning of the skin in man by sunlight, would be inherited to some extent by its offspring even in the absence of the particular environmental stimulus that produced it. Lamarck (1744–1829) thought that every animal would change in accordance with its needs. In part this was a semi-mystical conception, suggesting for instance that a shrew by trying to fly might become a bat, but it also included the supposition that the effects of use and disuse are inherited; an animal which ran fast would increase the size of its leg muscles and so would leave offspring which started with slightly better legs than their parent at the same age; a cave animal which did not use its eyes would have offspring with slightly smaller or weaker eyes, and so on. All these theories involve the inheritance of acquired characters, that is at least the partial transmission

to descendants of characters acquired during the lifetime of the individual. Darwin thought that this was possible, but unimportant. Later writers, including the earlier Mendelians, thought that it was theoretically impossible because the cytoplasm played no part in heredity and the germ-cell nuclei were isolated. This view is still widely held, and it is still sometimes said that it is difficult or impossible for us to conceive any means by which changes induced in the body during life could affect the germ cells. This is, however, not true, nor would it be a sound argument if it were. Many things happen every day, such as the falling of bodies to the earth, for which we have no mechanical explanation, and in fact the existence of hormones suggests a means by which any part of the body could influence any other part. There is no evidence that the germ cells are influenced in this way, but there is no reason why they should not be. Indeed, on the principle of Newton's second law and the principle of Le Chatelier, such influence is to be expected.

Many attempts have been made to test the hypothesis of the inheritance of acquired characters experimentally. Most have been inconclusive for one or more reasons. Those which have given negative results can be met with the suggestion that the work was not carried through enough generations ; few have lasted for more than five or six, which is negligible on the evolutionary time-scale. Those which have given positive results have either been susceptible of an alternative explanation in terms of selection, or have been repeated without success. In recent years, with the recognition by the geneticists of the importance of the cytoplasm in inheritance, new possibilities have emerged. It is generally agreed that induced characters can be inherited for several generations in the Protozoa, and there is at least the possibility that the same is true of the Metazoa ; this is, however, rather different from the directed production of mutations by the action of the environment.

The present theory of evolution may now be summarised. It accounts very satisfactorily, in terms of Mendelian inheritance, mutation, isolation and selection, aided perhaps by drift, for evolution within the genus, and brings together reasonably well a wide array of facts of taxonomy, ecology, distribution and behaviour. Its extension to the family and larger systematic units is progressively a matter of more and more extrapolation. In adaptive radiation at the ordinal level, as for example of

mammals (Chap. 25), we can see that the same processes may have been at work to produce the ancestors of each order as have produced the species within the order. Of the evolution of the phyla we know nothing, and can only assume, if we choose, that they have been produced in the same way. At every level above the lowest we need to explain the origin of new genes, and this we cannot do. The theory of evolution, though an admirable working hypothesis, still leaves the most important things unexplained.

INDEX

The first page only of an account is shown. Where there is more than one reference, italic type shows the most important.

Numbers in heavy type refer to pages with illustrations of the structure in question, but these are shown only where they are separated from the written account.

Abdomen of cockroach, 222
  of crayfish, 194
  of frog, **347**
  of rabbit, 417
Abdominal cavity, 417
  pores, 310, 322
Abomasum, **493**
Abscesses, 63, 75
Absorption, 7, 442
Acanthia lectularia, 252
Acanthias, 310, 311, 335
Acanthodii, **561**
Acarina, 236
Accommodation, 466
Acetabular facet, 320
Acetabulum of frog, 356
  of pigeon, 402
  of rabbit, 432
Acetylcholine, 621, 622
Acetylcoenzyme A, 536
Aciculum, 176
Acini, **513**
Acipenser, 552
Acquired characters, 734
Acromion, 355, 431
Acrosome, 633
Actin, 524
Actinia equina, 112
Actinopterygii, 551, 557, 561, 600
Actinozoa, 111
Actinula, 109
Activity, 6
Actomyosin, 525
Acusticolateralis system, 342
Adamsia palliata, 144
Adaptation, 14
Adaptive radiation, 239, 474, 495, 562
Adder, 556
Adrenal bodies or glands, 16, 536
  of dogfish, 343
  of frog, 366
  of rabbit, 470
Adrenaline, 16, 334, 470, 536, 622
Adult, 4, 245
Aedes, 145
Afferent, or sensory, fibres, 457, 619
Afterbirth, 672
Aftershaft, 393
Aglais urticæ, 255
Agnatha, 548, 559
Ague, 68
Air bladder, 551, *601*
Air capillaries of bird, 407
  cells, 444
  sacs, **406,** 407
Alæ cordis, 204
Ala spuria, 391
Albumen, 7, 659, 668
Alderfly, 253
Algæ, 20, 78, 506
Alimentary system, 595. And *see* Canal, alimentary
Alisphenoid canal, 429
Allantois, 665, 674
  of bird, 665
  of rabbit, 671
Allelomorphs, 693n, 707
Alligator, 609
Allolobophora, **155,** 156, 157, 161, 175
Alternation of generations, 105
  in *Aphis*, 252
  in liver fluke, 123
  in malaria parasite, 68
  in *Monocystis*, 42
  in *Obelia*, 105
  in tapeworms, 130
Alveolar layer in *Vorticella*, 56
Alveoli, 444, 513
Amblystoma, 684
Ambulacral groove of starfish, 287
Ameloblast, 511
Ametabola, 244
Amia, 600
Amino acids, 7, 441, 442, 443, 453, 504, 535
Amitosis, 51, 694
Ammocœte, 549
Ammonia, 8, 11, 119, 163, 210, 279, 291, 454, 535
Ammonites, 285
Amnion, 663, 674
  of bird, 663

Amnion of rabbit, 671
Amniota, 549, 663
Amniotic cavity, 663
Amœba, 24, 76, 78
discoides, 24, **30**
lescheræ, 24, **25**
proteus, 24, **26**
binary fission in ,32
encystment of, 33
excretion in ,28
irritability, automatism, and conductivity in, 27
movements of, 26
multiple fission in, 33
nucleus of, 24, 29, 713
nutrition of, 27
reproduction of, 32
respiration of, 28
spore formation in, 33
Amœbæ, multinucleate, 24
Amœbina, 78
Amœbocytes, 82, 161, 291, 292, 507, 518, 529
Amœboid movement, 26
Amœbulæ, 43n.
Amphibia, 553, 557
Amphidasis, 719
Amphineura, 283
Amphioxus, 298. *See* Lancelet
Amphiplatyan, 420
Amphistylic, 589
Amplexus, 378
Ampullæ of frog's ear, 386
of tube feet, 291
Amylase, 276, 441
Anabas, 602
Anabolism, 12
Anæmia, 136, 140
Anaerobic, 10, 11, 152
Anal cerci, of cockroach, 223
cirri, of *Nereis*, 176
Anaphase, 697, 702
Anapophysis, 422
Anapsid, **583**, 584
Anaspida, 557
Anatomy, definition of, 21
Ancylostoma duodenale, 140
Andalusian fowl, 692
Anemones, sea-, 111
Anguillula aceti, 138
Anguillulina tritici, 138
Anguina, 138
Anguis fragilis, 556, 562
Angular process, 429
Animal pole, 634n.
Animals, difference between plant and, 16
Anisogamy, 35
Ankle, **416**. *See* tarsus
Annelida, 155, *183*
Annuli of leech, 179
Annulus of Vieussens, 385
Anodonta, 270. *See also* Mussel, swan
Anomapsid, 585
Anopheles, 72, 145, **257**
Anopleura, 250
Ansa subclavia, 385
Ant-eaters, 496
Antebrachium, **416**
Antedon rosacea, 297
Antennæ of cockroach, 221, **223**
of crayfish, **196,** 198
Antennary glands, 210
Antennule of crayfish, **196,** 198, 214
Antibodies, 66, 149, 671
Anticoagulants, 68, 181
Anti-enzymes, 153
Antigens, 149
Antitoxins, 149
Antlers, 492
Ants, 144, 260, *263*
Anura, 555, 568, 587
Anus of *Ascaris*, 132
of cockroach, 223
of crayfish, 194
of dogfish, 310
of earthworn, 156
of frog, 346
of lancelet, 299
of *Nyctotherus*, 59
of pigeon, 405
of rabbit, 415
of snail, 264
of starfish, 288
of swan mussel, 276
of *Vorticella*, 57
temporary, of *Paramecium*, 49
Aorta, anterior and posterior, of cockroach, 228
of swan mussel, 279
branchial, of lancelet, 305
dorsal, of lancelet, 305
of chick, 667
of dogfish, 325
of frog, 371
of pigeon, **408**
of rabbit, 447
of vertebrates, 603
Aorta, ventral, of dogfish, 325
of frog, 368
of lancelet, 305
of vertebrates, 603
Aortic arches, **604,** 605, **606, 607, 610, 611**

Aortic arches of frog, 369
of pigeon, 408
of rabbit, 447
of tadpole, **612**
Aphaniptera, 259
Aphetohyoidea, 550
Aphis, 144, 239, 252
Apis mellifica, 261
Apoda, 555, 609
Apopyles, 82
Appendages of cockroach, 221
of crayfish, **196, 197,** 198
of vertebrates. *See* Limb, Limbs
mouth, of cockroach, **222**
of crayfish, **196,** 198
of insects, **240, 241, 242, 243**
Apteria, 392
Apterygota, 247
Apteryx, 412
Aquæductus cerebri or Sylvii, 616
of dogfish, 337
of frog, 383
of rabbit, 461
Arachnida, 235
Arachnoid, 538
Araneida, 235
Arboreal, 485, 496
Arborisation, terminal, of axon, 514
Arcades of skull, 584
Arcella, 78
Arch, pectoral. *See* Girdle, pectoral
pelvic. *See* Girdle, pelvic
Archæopteryx, **413,** 722
Archenteron, 636, 652, 654
Arches, aortic. *See* Aortic arches
of frog, 369
branchial, 316, 592, 656
hæmal, of dogfish, 314, 572
hyoid, of dogfish, 317
mandibular, of dogfish, 316
neural, 572
visceral, 592
of dogfish's skeleton, 316
Archiannelida, 185
Arcualia, 571
Area opaca and area pellucida, 661
Arenicola, 185
Argulus, 235
Aristotle, 717
Arm of man, **435**
of tetrapods, **416.** *See also* Limbs
Arteries, 447, 519, 543
of crayfish, 204
of dogfish, 325
of frog, **370**
of lizard, **613**
Arteries of pigeon,
of rabbit, **447, 448, 450**
of vertebrates, 605
Arterioles, 543
Artery, structure of, **13, 544**
afferent branchial, 325, 608
antennary, of crayfish, 205
anterior mesenteric, 328, 370, 447
brachial, 407
carotid, 326, 369, 407, 447
caudal, 328, 447
cephalic circle, 605
cœliac, 328, 371, 447
cœliacomesenteric, 370
common carotid, 325, 369, 447, 609
common iliac, 447
coronary, 447
cutaneous, 369
dorsal abdominal, of crayfish, 205
efferent branchial, 325, 608
epibranchial, 325, 608
external carotid, 327, 369, 447, 608, 609
external iliac, 447
gastric, of crayfish, 205
genital, 328, 447. *See also* ovarian, spermatic
hepatic, 328, 371, 447
of crayfish, 205
hyoidean, 328
iliac, 371
iliolumbar, 447
innominate, 407, 447
internal carotid, 326, 370, 447, 605, 609
internal iliac, 447
lienogastric, 328, 447
lingual, 369, 605
occipitovertebral, 370
œsophageal, 370
ophthalmic, 205, 605
optic, 605
orbital, 326, 370, 605
ovarian, 371
pectoral, 407
posterior mesenteric, 328, 371, 447
pulmonary, 369, 407, 447, 608, 609
renal, 328, 371, 447
segmental, 407
spermatic, 371
spiracular, 328
stapedial, 370, 605
sternal, of crayfish, 205
subclavian, 328, 370, 407, 447

Artery, suprabranchial, 305
systemic, 609
ventral abdominal, of crayfish, 205
thoracic, of crayfish, 205
vertebral, 603
vesical, 447
vitelline, 603, 667. *See also* Aorta, Aortic arches
Arthrobranchiæ, 209
Arthropod, 232
Arthropodin, 219
Articular process, 429
Articulation, 418
Artiodactyla, *492*, 563, 585
Ascaris, *131*, 140, 151, 152
alimentary canal of, 134
body wall, 132
excretory organs of, 133
generative organs of, 135
infective larvæ of, 136
lumbricoides, 131, 132
megalocephala, 131
muscle fibres of, **135**
nervous system of, 134
sperm of, 633
suillæ, 131, 132
Ascon, 84
Asexual reproduction. *See* Reproduction, asexual
Assimilation, 7, 10
Astacus pallipes, 194. *See also* Crayfish
Aster, 633
Asterias rubens, 286. *See also* Starfish
Asteroidea, 296
Atlas, 349, *421*
Atriopore, 299
Atrium of lancelet, 299
Atrium = auricle, *see* Heart
Atropas, 250
Auditory capsules, 316, 351, 400, 423, 424, 425, 579, 582
organs. *See* Ear
ossicles, 592
placode, 626
Aulostomum, 185
Aurelia, 109, **110, 111**
Auricle, 324. *See* Heart
Autogamy, 54
Automatism, 7
in *Amœba*, 27
in *Paramecium*, 49
Autonomic system, 385, **461,** 462, *621*. *See also* Sympathetic system
Autosomes, 709
Autostylic, 589
Autotomy, 43, 202
Aves, 556
Avoiding reaction, 49
Axial organ of starfish, 289, 293
Axis cylinder, 515
of the body, factors determining, 634, 683
vertebra, 421
Axon, 514

Backbone. *See* Vertebræ
Bacteria, 21, 225
rôle of, in digestion, 225, 442, 491, 492
Badger, 489
Balænoptera, **486,** 487
Balance of nature, 20
Balancers, 244
Balanoglossus, 308, 557
Balantidium coli, 75
entozoon, 59
Balanus, 235
Baleen, 486
Barbicels, 392
Barbs of feather, 392
Barbules, 392
Barnacle, 235
Bars, gill and tongue, of lancelet, 302
Basal body, 39, 46, 47, 64
Basal metabolic rate, 470
Basal nucleus, 618
Basement membrane, 520
Basilar membrane, 467
Basipodite, **196**
Basipterygium, 320
Bastard wing, 391, 392
Bat, wing of, **727**
Bateson, W., 691, 693
Bath sponge, 85
Bats, *477*, 565
Bdellostoma, 627
Beak, 390, 401
Beans, 253
Bears, 488
Beaver, 485, 486
Bed bug, 145, 243, 252
Bees, 144, **243,** 245, *260*
Beetles, 239, 244, 245, *260*
Behaviour of *Amœba*, 27
of *Hydra*, 94
of *Paramecium*, 49
Bell animalcules, 55
Bichart, M. F. X., 506
Bilateral symmetry, 102, *187*
Bile, 442, 536
Bile duct of dogfish, 322

Bile duct of frog, 363
of man, **481**
of pigeon, 405
of rabbit, 438
Bilharzia, 124
Binary fission. *See* Fission
Biogenetic law, 724
Biological races, 154
Biology, definition of, 1
Bipinnaria larva, 294
Biramous limb, 197
Bird lice, 150, *250*
Birds, 250, *556*, 557, 585, 618, 625. *See* Aves
and reptiles, 413
Biston betularia, 719
Bladder, air, 551, 600
gall, of dogfish, 322
of frog, 363
of rabbit, 438
salivary, of cockroach, 225
urinary, 512, 630
of frog, 363, 370
of rabbit, 453
Bladder-worm, **125**, 127, **130**
Blastocœle, 636
of chick, 660
of frog, 650
of lancelet, 643
of trochosphere, 178
Blastocyst, 668
Blastoderm, 658, 660
Blastodisc, 657, 659
Blastomeres, 636
of Amphibia, potentialities of, 675
of frog, 629
of *Hydra*, 97
of lancelet, 641
Blastopore, 636
of chick, 663
of frog, 653
of lancelet, 643
of mammals, 663
Blastostyles, 104
Blastula, 636
of crayfish, 671
of frog, 629
of *Hydra*, 97
of lancelet, 641
of liver fluke, 122
of *Obelia*
of starfish, earthworm, and swan mussel, 670
Blatta orientalis, 218, 222, 223, 230
Blatella germanica, 218, 230
Blepharoplast,
Blind spot, 464, 540
Blind-worm, 556
Blood, 452, *528*
functions of the, 189
islands, 659
of crayfish, 207
of dogfish, 329
of earthworm, 163
of frog, 373
of lancelet, 305
of leech, 182
of man, 528
of pigeon, 407
of rabbit, 452
of swan mussel, 279
See also Respiration
Blood-vascular system, 188, 190, 666. *See also* Arteries, Vascular System, Veins
Blow-flies, 240, *259*
Bluebottles, 259
Blushing, 190
Body cavities, 187. *See also* Cœlom, Hæmocœle
cavity, primary, 188
secondary, 189
fluids, 508
-wall, **571**
of earthworm, 158
of *Hydra*, 87
Bojanus, organs of, 278
Bone, 521
cartilage and membrane, 522
marrow, 521, *531*
Bone or bones—
alisphenoid, 400, 423, 425, 581, 588
angular, 401, 592
angulosplenial, 353, 592
articular, 401, 591
astragalus, 435, 562
autopalatine, 588
basihyal, 592
basioccipital, 399, 423, 582
basisphenoid, 400, 423, 581
basitemporal, 400
calcaneum, 435, 562
calcar, 357
cannon, 492
capitate, 562
carpal, 356, 402, 432, 562
central, 562
ceratohyal, 592
clavicle, 355, 401, 432, 566
cleithrum, 566
coccyx, **480**
columella auris, 352, 354, 401, 592
coracoid, 354, 401, 431, 568
coronoid, 592

Bone or bones—coxa, 432
cuboid, 562
cuneiform, 562
dentary, 353, 401, 428, 592
dermosupraoccipital, 585
distal carpal, 562
tarsal, 562
ectocuneiform, 562
ectopterygoid, 427, 591
entocuneiform, 562
epihyal, 592
epiotic, 582
epipterygoid, 588
ethmoid, 480
exoccipital, 350, 399, 423, 582
femur, 357, 403, 432, 564
fibula, 403, 432, 562
fibulare of ankle, 357, 435, 562
frontal, 400, 424
frontoparietal, 350
gulars, 583
hamate, 562
humerus, 356, 402, 432, 564
hyoid, 354, 401, 430
hyomandibula, **581**
ilium, 356, 402, 432, 567
incus, 426, 594
innominate, 432, 569
interclavicle, 402, 566
intermediate (intermedium) of carpus, 357, 562
interopercular, **581**
interparietal, 424, 585
intertemporal, 587
ischium, 356, 403, 432, 567
jugal, 427, 591
lacrimal, 400, 424
lunar, 562
lunate, 562
magnum, 562
malar, 427, 591
malleus, 426, 428, 594
maxilla, 353, 401, 427, 591
mentomeckelian, 353, 591
mesethmoid, 350, 400, 423, 580
mesocuneiform, 562
metacarpal, 357, 402, 432
metapterygoid, **581**
metatarsal, 403, 432
nasal, 352, 401, 426
navicular, 562
opercular, 583
opisthotic, 582
orbitosphenoid, 400, 423, 425, 581
palatine, 353, 401, 426, 591
parasphenoid, 350, 400, 587
parietal, 400, 424
patella, 435
Bone or bones—periotic, 400, 425, 582
petrosal, 425, 582
phalanges, 403, 432
pisiform, 435
pleurosphenoid, 581
ploughshare, 395
postfrontal, **583**
postorbital, **583**
prearticular, 401, 592
precoracoid, 567
prefrontal, 582
premaxilla, 353, 401, 428, 591
preopercular, **581**
presphenoid, 400, 423, 581
prevomer, 352
pro-otic, 582
pterosphenoid, 581
pterotic, 582
pterygoid, 353, 401, 426, 427, 588, 591
pubis, 403, 432, 567
quadrate, 353, 401, 426, 588
quadratojugal, 353, 401, 591
radial (radiale), 357, 402, 562
radio-ulna, 356
radius, 402, 434, 562
scaphoid, 562
scapula, 354, 401, 431, 567
semilunar. *See* lunate
sphenethmoid, 350, 582
sphenoid, 480
sphenotic, 582
splenial, 401, **591**
squamosal, 352, 400, 425
stapes, 426, 594
subopercular, **581**
supraoccipital, 399, 423, 582
suprascapula, 354
supratemporal, 585
surangular, 401, 592
symplectic, **581**
tabular, 585
talus, 432, 562
tarsal, 359, 403, 432, 562
temporal, 480, 582
tibia, 403, 432, 562
tibiale, 359, 562. *See also* Astragalus
tibiofibula, 357
trapezium, 562
trapezoid, 562
triquetral, 562
turbinal, 426
tympanic, 426, 475, 592
ulna, 402, 434, 562
ulnar (ulnare), 357, 402, 562
unciform, 562

Bone or bones—vomer, 352, 401, 426, 587
Weberian, 601
Wormian, 480
zygomatic. *See* Jugal
See also Girdle, Rays, Ribs, Skeleton, Sternum, Vertebræ
Bony fishes, 193, *551*
Book-louse, 250
Boophilus annulatus, 236
Bos taurus, 492
Botany, 21
Botflies, 259
Botryoidal tissue, 179, 182
Bowman's capsule, **376**, 453, *627*
Brachiolaria larva, 294
Brachium, 415
Brain, 616, **617**
box, 315, *423*
of cod, **618**
of crayfish, 210
of dogfish, 335
of earthworm, 165
of frog, 383
of insects, 228
of liver fluke, 119
of pigeon, 412
of rabbit, 458
of Turbellaria, 128
See also Ganglia, cerebral
Branchiocardiac groove, 195
Branchiopoda, 234
Branchiostegite, 195
Branchiostoma, 298. *See* Lancelet
Breastbone, 422 ; *see* Sternum
Breathing, 374, 407, 444
Bridges, C. B., 706
Bristles, 197
Bristle-tails, 247
Brittle stars, 296
Bronchi, 511, 537
of frog, 374
of pigeon, 406
of rabbit, 444
Bronchioles, 444, 513
Brown, Robert, 498
Brown tubes, 304
Buccal cavity, 435, 595
Buccinum, 284
Budding, 4
of *Carchesium*, 58
of *Hydra*, 98
of *Obelia*, 104, 105
of Protozoa, 58
of *Vorticella*, 57
Buffon, Comte de, 718, 734
Bufo, 555. *See* Toad
Bugs, 251
Bulla, 426
Bunodont teeth, 480, 489
Bursa Fabricii, 405
Butterflies, 242, 244, 245, *253*
B-vitamins, 9, 10, 536
Byssus, 281

Caddis-flies, 253
Cæca, lateral, of leech, 181
pyloric, of cockroach, 226
of starfish, 289
rectal, of pigeon, 405
of starfish, 291
Cæcilia, **554**
Cæcum of crayfish, 204
of man, **482**
of rabbit, 438, 442
of swan mussel, 276
Calamus, 392
Calcium carbonate, 81, 112, 161, 185, 197, 264, 266, 287, 296
Calcium phosphate, 521
Calf, fore-leg of, **493**
Calliphora, 259
Camels, *492*, 519, 529
Canal or canals—
alimentary—
histology of, 533
origin of, in chick, 662
in lancelet, 643
in tadpole, 654
of *Ascaris*, 132
of cockroach, 224
of cod, **630**
of crayfish, 202
of dogfish, 320
of earthworm, 158
of frog, 360
of lancelet, 301
of leech, 181
of liver fluke, 115
of *Nereis*, 177
of pigeon, 403
of rabbit, 435
of snail, 267
of starfish, 290
of swan mussel, 275
circular. *See* ring
hæmal, 314
Haversian, 521
Laurer-Stieda, 115, 120
neural, 636
neurenteric, 644, 654
pericardio-peritoneal, 320
radial, 102
ring, 102
semicircular, 342, 386, 468

Canal or canals, stone, 289, 291
  systems, of sponges, 83, 84
  urogenital, 454, 456
  vertebrarterial, 421
Canaliculi of bone, 522
Canis familiaris, 488
  lupus, 488
Cannon bones, 492
Capillaries, **372,** *445*, 452, 543
Capitosaurus, **584**
Capitulum, 422
Capreolus capreolus, 492
Capsules, egg, 230
  nasal and auditory, 315, 351, 400, *423*, 425, 426, 578, 579, 582, 584, 587
  optic, 423
Carapace, of crayfish, 195
Carapus, 146
Carbohydrates, 8, 10, 18, 442
  See also Glycogen, Paraglycogen, Paramylum, Starch, Sugar
Carbon dioxide, 10, 15, 18, 452
Carchesium, 59
Cardo, **222**
Carina, 402
Carnivora, 487
Carnivores, 145
Carotid labyrinth, 370, 609
Carp, **551**
Carp louse, 235
Carpometacarpus, 403
Carpopodite, **196**
Carpus, 356, 402, **416,** 432, *562*, 563
Carteria, 93
Cartilage, 520
Cartilage bones, 522
Cartilage or cartilages—
  acrochordal, 579
  arcualia, 571
  arytenoid, 374, 444, 592
  basal, 318, 320
  basibranchial, 316, 588, 592
  basidorsal, 571
  basihyal, 318, 592
  basiventral, 571
  branchial, 588
  ceratobranchial, 316, 592
  ceratohyal, 318, 588, 592
  cricoid, 444, 592
  epibranchial, 316, 588, 592
  epicoracoid, 354
  epiglottal, 592
  extrabranchial, 318
  hyoid, 588
  hyomandibular, 317, 589, 592
  hypobranchial, 316, 588
  interdorsal, 571
Cartilage—interventral, 571
  ischiopubic, 320
  labial, 318
  Meckel's, 587
  of dogfish, 316
  of frog, 353
  of mammal, 428
  mesethmoid, 316
  orbital, 579
  palatopterygoquadrate, 316, 426, 587
  parachordal, 579
  pharyngobranchial, 316, 588
  polar, 579, 587
  procoracoid, 355
  pubic, 356
  radial, 318, 320
  scapulocoracoid, 318
  supradorsal, 573
  suprascapular, 432
  trabecula, 579, 587
  tracheal, 444
  thyroid, 444, 592
  xiphoid, of frog, 355
    of rabbit, 423
Cartilaginous fishes, 193, 550
Castor fiber, 485, 486
Catastrophism, 718
Caterpillars, 245, **254**
Cats, 119, 431, *488*, 532, 563, 712
Cattle, 492
Cauda equina, 382
Caudal vertebræ, 422
Cell division, 700
  walls, 501, 638
Cells, **13,** *498*, 501, 508
  blood, 528
  bone, 521
  chloragogenous, 161
  connective tissue, 517
  dendritic, 532
  epithelial, 509
  fat, 519
  flame, 118, 304
  germ. *See* gametes
  gland, 512
  goblet, 512
  muscle, 526
  musculo-epithelial, 87
  nerve, 508, 514
  of *Hydra*, 87, 93
  of Rauber, 671
  pigment, 347, 532
  pole, 679
  red, 373, 407, *528*
  Schwann, 515
  sense, of earthworm, 171
  sensory, **541**

Cells, white, 373, *528*
  yellow, 161, 163
  zymogen, 512
Cellulose, 20, 309
  digestion of, in herbivores, 442
Cement, 437, 523
Cement layer 220
Centipedes, 237
Centromere, 700
Centrosome, 502
Centrum, 419, 572
Cephalaspida, 523, 557
Cephalaspis, 560
Cephalisation, 192
Cephalochordata, 308
Cephalopoda, 192, *285*
Cephalothorax, of crayfish, 195
  of spiders, **236**
Cercariæ, 123
Cere, 390
Cerebellum, 616
  of dogfish, 337
  of frog, 383
  of pigeon, 412
  of rabbit, 460
Cerebral convolutions, 458
  hemispheres, 616
    of frog, 384
    of pigeon, 412
    of rabbit, 458
  sulci, 458
Cerebrospinal axis, 457
  fluid, 539
  nerves, 457
  system, 457
Cerebrum, of dogfish, 336
Cervical vertebræ, 421
Cervus elaphus, 492
Cestoda, *129*, 150
Cetacea, 486
Chætæ of earthworm, **157,** 167, 175
  of *Nereis*, 175
Chætopoda, 183, **184**
Chætopterus, 638
Characters and chromosomes, 704
Cheiroptera, 475, *477*
Cheiropterygium, **416,** 561
Chelicerae of spiders, 235
Chelicerata, 235
Chelipeds, 198
Chelonia, 556, 584, 609, 613
Chemical work in the body, 11
Chest, 417
Chiasma, of chromosomes, 700
  optic, of dogfish, 342
Chick, development of, 659
Chilopoda, 237
Chin, 480
Chironectes, 495
Chironomidæ, 259
Chiroptera. *See* Cheiroptera
Chitin, 101, 136, *157*, 161, 197, 219, 226
Chiton, 283
Chlamydomonas, **19,** 20, 35, 78
  syngamy in, 35
Chlamydospores, 43n
Chloragogenous cells, 161
Chlorohydra viridissima, **86,** 93, 96, 144
Chlorophyll, 17, 18
Chloroplasts, 17
Choanichthyes, 552, 557
Choanocytes, 81, 84
Choanoflagellata, 38
Cholesterol, 532
Cholinergic, 622
Chondrichthyes, 550
Chondrin, 520
Chondroblasts, 520
Chondrocranium, 578
Chordæ tendineæ, 368
Chordata, 146, 308
Chorioallantoic membrane, 665
  placenta, 671
Chorion, 663, 668, 671
Choroid coat, 464, 542
  fissure, 623
  plexus, 383, 384, 618
Chromatids, 696
Chromosomes, 503, 696
Chrysopa, 253
Chrysops, 142
Cilia, 39, **46,** 274, 275, 302, 505
Ciliary body, 464
Ciliata, 45, 80
Ciliophora, 79
Cimex lectularius, 145, 252
Ciona, 309
Circulation of the blood, regulation of, 446
Circulatory system, 602. *See also* Vascular system
Cirri of lancelet, 299, 301
  of *Nereis*, 176
Cirripedia, 235
Cirrus of liver fluke, 119
  sac, 119
Cladoselache, 559, 560
Clasper, 312, 320, 334
Class, 22, 717
Classification, 22, 715
Clavicles of frog, 355
  of pigeon, 401
  of primates, 478, **568**
  of rabbit, 432

Clavicles of vertebrates, 568
Claws, 533
Cleavage of ovum, 636
  complete or holoblastic, 636
  determinate, 638
  indeterminate, 638
  mosaic, 638
  radial, 650
  spiral, 638, *676*
  of bird, 659
  of frog, 641
  of *Hydra*, 97
  of invertebrates, 676
  of lancelet, 638, 641
  of rabbit, 668
Clegs, 259
Cleidoic eggs, 556
Climatius, **561**
Cline, 731
Clitellum, 156, 174
Clitoris of rabbit, 415, 456
Cloaca, 636
  of dogfish, 323
  of frog, 363
  of Monotremata, 496
  of pigeon, 410
  of rabbit, 453
Clone, 54, 107
Closed blood system, 188
Clotting of blood, 528
Clypeus, 221
Cnemial crest, **433**
Cnidaria, 107
Cnidoblasts, 88, 89, 90
Cnidocil, 88
Cnidosporidia, 76, 79
Coccyx, **480**
Cochlea, 412, 467
Cockle worm, 138
Cockroach, 244, 249, *218*
  abdomen of, 222
  alimentary system of, 224
  blood vessels of, 227
  digestion and excretion in, 225
  head of, 221
  locomotion of, 223, **226**
  mouth appendages of, 221
  nervous system of, 228
  reproductive organs of, 229
  respiratory organs of, 227
  sense organs of, 228
  thorax of, 221, **226**
Cocoon, 175, 183, 254
Cod, 552, **566, 581, 599, 604, 608, 610, 618, 630**
Cœfficient of friction, 418
Cœlenterata, 86, 107
Cœlom, 187
  of arthropods, 232
  of bird, 661
  of crayfish, 210
  of dogfish, 320
  of earthworm, 158
  of frog, 652, 655
  of lancelet, 300, 648
  of leech, 182
  of rabbit, 417
  of snail, 268
  of starfish, 288, 292
  of swan mussel, 275
Cœlomate body, 186
Cœlomic epithelium of earthworm, 158
    See also Peritoneum
  fluid, 187
Cœlomoducts, 188, 209, 268, 278, 330, 626
Cœnocyte, *499*
Cœnosarc, 101
Cœnurus cerebralis, 130
Coenzymes, 471, 536
Coition, 6, 411, 455
Coleoptera, 260
Collagen, 81, 132, 157, 285, 517
Collar, 264, 266
  cells, 81, 82
Collembola, 247
Colliculi, 460
Colon of cockroach, 225
  of rabbit, 439
Colonies, 58
Colpidium, 27
Columba, 389. *See* Pigeon
Colour changes in frog, 347
Columella auris, 352, 354, 401, 592
Columella of Mollusca, 266
Columnæ carneæ, 366
Combustion of carbohydrates and fats, 10
Commensalism, 144
Commissures, cerebral and cerebropedal, of mussel, 280
  circumœsophageal, of cockroach, 228
    of crayfish, 210
  circumpharyngeal, of earthworm, 165
    of leech, 182
  visceral, of mussel, 281
Competence, 686
Conchiolin, 266
Concretion, calcareous, round spinal nerve, 380
Conduction, 11
  in nerve, 620

Conduction in nerve net, 91
Conductivity, 12
Condyle, occipital, 350, 423. *See also* Skull
Cone, oral, 87, 93
Cones of retina, 540
Conies, 491
Conjugants, 51
Conjugation, 6, 51
in Ciliata, **52**
of *Paramecium*, 51
of *Vorticella*, 57
Conjunctiva, 464
Connective tissue, 517
Contractile fibre of *Vorticella*, 56
processes of cells of *Hydra*, 87
Contraction, 11
Conus arteriosus, 603. *See* Heart
Convergence, 484
Convolutions, cerebral, 458
Copepoda, 234
Coprodæum, 405
Copromonas, **4**
Copulation, *6*, 120, 173, 269, 334, 455
Coracoid process, 431
Corals, 112, 148
Cord. *See* Spinal cord, Nerve cord, Spermatic cord, Vocal cords
Corium, 532
Cornea, 542, 625
of crayfish, 212
of sheep, 464
Cornua, of hyoid, 354
Corona radiata, 668
Coronella austriaca, 556
Coronoid process, 429
Corpora allata, 220, 246
quadrigemina, 460
striata, 384, 412, 459, 618
Corpus albicans, or mammillare, 460
callosum, 458
luteum, 676
Corpuscles, blood, 528. *See also* Blood
bone, 521
connective tissue, 517
Cortex, cerebral, in rabbit, 458
of adrenal bodies, 366
of green glands, 210
of kidney, 545
of *Paramecium*, 47
Corti, organ of, 467
Costa of wing, 224
Costal pit, 422
Cotylosauria, 584
Coverts, 392
Coxopodite, **196**
Crab, hermit, 144
Crab-louse, 145, 250
Crabs, 234
'Crabs' eyes,' 204
Crane-flies, 259
Cranial nerves. *See* Nerves, cranial
Craniata, 548
Cranium, 315, *423*. *See also* Skull
Crawling, 357. *See also* Locomotion
Crayfish, *194*, 234
abdomen of, 194
alimentary system of, 202
blood vessels of, 204
cœlom of, 210
cuticle of, 194, 197
development of, 216, 680
epidermis of, 197
excretory organs of, 209
eye of, 195, *212*
gills of, 208
habits and external features of, 194
limbs of, 195, **196,** 198
locomotion of, 200
mouth appendages of, **196,** 197
nervous system of, 210
reproduction of, 215
respiratory organs of, 208
segments of, table of, 198
sense organs of, 212
skeleton and muscles of, 200
Creation, 718
Creodonts, 487
Crest, cnemial, **433**
Cribriform plate, 423, 580
Crickets, 248
Crinoidea, **296,** 297
Crithidial phase, 67
Crocodile, 555
skull of, **586**
Crocodilia, 556, 585, 612, 613
Crop of cockroach, 225
of earthworm, 161
of leech, 181
of pigeon, 403, 596
of snail, 267
Crossing-over, 702, 705, 706
Crossopterygii, *552*, 588, **722**
Crura cerebri, 383, 460
Crus, **416**
Crustacea, 232
Crystalline style, 276
cone, **213**
Ctenidia, 284
Ctenophora, 112
Cubitals, 391
Cuckoo, 146
Culex, 142, **241** **257**

Cursorial, 564
Cuticle of Arthropoda, 232
of *Ascaris*, 132
of crayfish, 194, 197
of earthworm, 157
of insects, 219
of leech, 179
of *Polytoma*, 34
Cuticulin, 220
Cuttlefish, 285
Cuvier, G., 718
Cuvierian sinus, 613
Cyanea aurita, 109
Cyclops, **234**, 235
Cyclostomata, 549
Cypris, **233**, 234
Cyst of *Amœba*, 33
of *Cercaria*, 123
of *Entamœba*, 61, 64
of *Monocystis*, 43
of *Opalina*, 60
of *Polytoma*, 35
of *Trichinella*, 142
Cysticercus, **125**, 127, 130
Cytochrome, 502
Cytogamy, 54
Cytophore, 173
Cytoplasm, 499, 683
Cytoplasmic inheritance, 713
Cytoproct, 49, 57, 59
Cytostome of *Paramecium*, 46
of *Vorticella*, **56**

Dactylopodite, **196**
Daddy-long-legs, 259
Dama dama, 494
Daphnia, **233**, 234
Dart sac, 269
Darwin, C. R., 156, 718
Darwin, E., 718
Dasyurus, 495
Dauermodificationen, 714
Deamination, 8, 535
Death, 499, 500
Deer, 492
Degrowth, 1, 129
Delhi boil, 60
Deltoid ridge, 356
Deme, 733
Demodex folliculorum, 236
Dendrites, 514
Dendrocœlum lacteum, 129
Dendrons, 514
Dental formula, 437
Dentalium, 284
Dentine, 312, 436, 523
Deoxyribonucleic acid (D.N.A.), 64, 503, 504, 707
Depression—
in *Amœba*, 32
in *Hydra*, 96
in *Paramecium*, 54
Dermaptera, 249
Dermatome, 665
Dermis, 347, 532
Dermotrichia, 318, 320
Determination, 637, 676, 681, 683
of sex, 687, 709
Deutoplasm, 499
Development, 4, 632
of birds, 659
of crayfish, 680
of dogfish, 334
of earthworm, 679
of frog, 649
of *Hydra*, 97
of insects, 680
of invertebrates, 676
of lancelet, 640
of liver fluke, 122
of mammals, 673
of man, **675**
of molluscs, 676
of *Obelia*, 104
of polychaetes, 676
of rabbit, 668
of tunicates, 681
See also Life-history
Diademodus, 560
Diakinesis, 702
Diapedesis, 530
Diaphragm, 417, 444
Diapsid, 585, 612
Diarrhœa, 136, 147
Diarthrosis, 545
Diastema, 437
Diastole, 29
Dictyoptera, 249
Dictyosome, 77
Didelphis, 496
Diencephalon, 616
Differences between animals, 14
animals and plants, 16
parents and offspring, 3
Differentiation, 14, 683
Difflugia, **78**
Digestion, 7
external, 235, 290
in *Amœba*, 27
in cockroach, 225
in crayfish, 204
in dogfish, 323
in earthworm, 161
in frog, 364
in *Hydra*, 95
in lancelet, 303

Digestion in mussel, 276
 in *Paramecium*, 49
 in pigeon, 405
 in rabbit, 440
 in snail, 268
 in spider, 235
 in starfish, 290
Digestive diverticula, 204, 210, 267, 275, 303
 organs. *See* Canal, alimentary
Digitals, 391
Digitigrade, 415, 489, 563
Digits, 415
Dimastigamœba, 79
Dimorphism of gametes, 5
Dinosaurs, 562, 585
Dipeptides, 441, 443
Diphosphopyridine nucleotide (DPN), 536
Diphycercal, 559
Diploblastica, 107, 186
Diploid, 702
Diplopoda, 237
Diplotene stage, 700
Diplura, 247
Dipnoi, *552*, 589, 596, 600
Diptera, 145, 244, *255*
Disaccharase, 441
Discus proligerus, 546
Disc of starfish, 286
 of *Vorticella*, 55
Discs, imaginal, 246
Distal, 187
Distomum hepaticum, 115
Division, amitotic, 702
 meiotic, 700
 mitotic, 696
 of *Amœba*, **30, 31,** 32
 of cells, 700
 of nuclei, 696
 of *Paramecium*, 51
 reduction, 700
 See also Fission
Dobell, C., 76, 77
Docodonts, 594
Dog, 532, 563, **564**
 skull of, *423*, 585
Dogfish, *310*, 550, 559
 alimentary system of, 320
 backbone of, 314
 blood vessels of, 324
 brain of, 335
 cranial nerves of, 340
 ductless glands, 343
 excretory organs of, 329
 external features of, 310
 gill arch of, **599**
 heart of, 324
Dogfish, limbs of, 318, 560
 muscles of, 312
 nervous system of, 335
 reproduction, 333
 respiration of, 323
 sense organs of, 342
 skeleton of, 314
 skin of, 311
 skull of, 315
 swimming of, 313
 veins of, **614**
 water regulation, 333
Dogs, 488
Dolphins, 486
Dominance, 689, 708
Doralis rumicis, 252
Dormouse, 485
Dorsal lip, 643, 650, 658, 663, 683
 pores, 158
 surface, 187
Down, 393
Dracunculus medinensis, 141
Dragon-flies, 239, 245, *248*
Drift, 733
Drones, 261
Drosophila, **696,** 704
Drugs, effect of, on *Paramecium*, 49
Duck-billed platypus, 496, 585
Duct, bile, 535
  of dogfish, 323
  of frog, 363
  of man, **481**
  of pigeon, 405
  of rabbit, 438
 carotid, 609
 ejaculatory, or *Ascaris*, 135
  of cockroach, 229
  of liver fluke, 119
 hermaphrodite, 269
 holonephric, 627, 629
 mesonephric. *See* Duct, Wolffian
 metanephric. *See* Ureter
 Müllerian, 629, 631
 pancreatic, of dogfish, 323
  of man, **481**
  of pigeon, 405
  of rabbit, 438
 pronephric, 627, 631, 687
 segmental, 626
 thoracic, 530
 urinary, 333
 Wolffian, 629, 687
  of dogfish, 331, 333
  of frog, 376, 378
Ductless glands. *See* Glands, ductless
Ductus arteriosus, 447, 609

Ductus Botalli, 609
Cuvieri, 305, 328, 667
deferens. *See* Vas deferens
endolymphaticus, of frog, 387
of rabbit, 468
Dung, 10
Duns Scotus, 717
Duodenum, of dogfish, 322
of frog, 363
of man, **481**
of pigeon, 405
of rabbit, 438
Duplicidentata, 484
Dura mater, 519, 538
Dysentery, 64, 75
Dytiscus, 220, 245

Ear, of bird, 412, 626
of dogfish, 342
of frog, 386, 626
of insects, 249
of rabbit, 466
of teleost, 626
origin of, 625
ossicles, 466, *594*
Earthworm, 155
alimentary canal of, 158
body-wall of, 158
burrowing of, 168
circulation of, 163
development of, 679
excretion in, 163
external features of, 156
openings of, 157
food of, 156
habits of, 155
histology of, **160**
movement of, 166
nephridium of, **162,** 163
nervous system of, 165, **167,** 168
pairing of, **155,** 173
regeneration in, 175
reproduction of, 171
reproductive organs of, **184**
section of, **159, 171**
sense organs of, 171
Earwigs, 249
Ecdysis, 200, 220, *246*
Echidna, 496
Echinococcus, 130
Echinodermata, 286, *295*, 557
Echinoidea, 296
Echinus esculentus, 297
Ectoderm, 186, 637
of *Hydra*, 87
See also Epiblast, Epidermis
Ectoparasite, 146, 150, 236
Ectoplasm of *Amœba*, 24, 26
Ectoplasm of *Entamœba*, 61
of *Monocystis*, 41
of *Paramecium*, 46
of *Vorticella*, 56
Eel, 602
Egg, 5, 659. *See also* Ovum
sac of earthworm, 172
Eimeria, 148
Elasmobranchii, 550, 558, 560, **633**
Elastic fibres, 517
Elastin, 318, 517
Electron microscope, 501
Elephantiasis, 142
Elephants, 491
Elytra, 244
Embioptera, 249
Embryo, 632
Embryology, 632. *See also* Development, Life-history
Embryonic circulation of chick, 666
membranes, 663. *See also* Allantois, Amnion
Empusa muscæ, 259
Enamel, 312, 436, 511
Encystment. *See* Cyst
End sac of crayfish, 210
Endergonic reactions, 10
Endocrine organs. *See* Glands, ductless
Endocuticle, 219
Endoderm, 186, 637
of *Hydra*, 87, *93*
See also Hypoblast
Endolymph, 386, 467
Endomixis, 54
Endoneurium, 515
Endoparasite, 146, 151
Endophragmal skeleton, 200
Endoplasm of *Amœba*, 24, 26
of *Monocystis*, 41
of *Paramecium*, 46
of *Vorticella*, 56
Endoplasmic reticulum, 502
Endopodite, 197
Endopterygota, 245, *253*
Endostyle, 302
Endothelium, 543
Endothermic reactions, 10
Energy, 10
forms of, 11
Energy-producing factors in food, 8
storage of, by plants, 20
Entamœba coli, **61**
histolytica, **61,** 62
Enterobius, 143
Enterocœle, 648
Enterokinase, 443

Enteron, 645
of *Hydra*, 87
of *Obelia*, 101
See also Archenteron
Enteropneusta, 308
Entypy, 674
Eogyrinus, **567, 591**
Environment, effect of, 682, 707
Enzymes, 9, 471, 502, 707
Eohippus, **720**
Ephemeroptera, 248
Ephyra, 110
Epiblast, 186, 637, 660
Epicranial plates of cockroach, 221
Epicuticle, 220
Epidermis, 510, 532
of crayfish, 197
of earthworm, 157
of frog, 347
of leech, 179
of liver fluke, 116
of rabbit, 416
Epididymis, 454, 547
of leech, 182
Epigenesis, 634
Epiglottis, 437, 520
Epimere, 648, 655
Epimeron, 195
Epineurium, 539
Epipharynx, 221, 238
Epiphragm of snail, 266
Epiphysis, 420
Epipodite, 197
Episternum, 355
Epistylis, 59
Epitheliocyte, 507
Epithelium, 508, 509
germinal, 513
sensory, 514, 540
Epizoon, 144
Equus, 491, **720**
Erection, 190, 334, 455, 471, 623
Erinaceus europæus, 476
Erithacus rubecula, 717
Erythrocyte, 528
Erythrocytic cycle, 69
Escargot, 264
Euglena, 20, *36*, 78
gracilis, **36,** 38
viridis, 37
Euonymus europæa, 252
Eupagurus prideauxi, 144
Euryhaline animals, 193
Euspongia officinalis, 85
Eustachian tube, 362, 387, 436, 467, 520, 598, 626
Eutheria, 474
Evocator, 685
Evolution, 718
evidence for, 719
mode of, 728
Exconjugants, 53
Excretion, 11, 12
Excretory organs, 193, *626*
of *Ascaris*, 133
of chick, 665
of cockroach, 227
of crayfish, 209
of dogfish, 329
of earthworm, 163
of frog, 375
of lancelet, 304
of leech, 181
of liver fluke, 118
of pigeon, 410
of rabbit, 453
of snail, 268
of swan mussel, 278
of tadpole, 627
of tapeworm, 126
See also Kidneys
Exergonic reactions, 10
Exocuticle, 219
Exoerythrocytic cycle, 69, 72
Exopodite, 197
Exopterygota, 245, *248*
Exoskeleton, 200
Exothermic reactions, 10
External auditory meatus, 426
Exteroceptive, 619
Exumbrella, 101
Eye muscles of dogfish, 342
of frog, 385
Eyelashes of rabbit, 414
Eyelids of frog, 344
of pigeon, 390
of rabbit, 414
Eyes of Anura, **386**
of birds, 412
of cockroach, 228
of crayfish, 212
of frog, 385
of *Miracidium*, 122
of molluscs, 269
of *Nereis*, 176
of sheep, 464
of vertebrates, 540, 623
Eyespot. *See* Stigma

Facet for rib, 422
glenoid, 318
of ribs, 422
Facilitation, 92
Fæces, 10, 442
Falciform ligament, 438, 597
Fallopian tubes, 456

Family, 22, 717
Fasciæ, 517
Fasciculi, 526
Fasciola hepatica, *115*, 129, 151
Fat bodies, of frog, 366
Fate map, 639, 650
Fatigue, 92
Fats, 8, 10, 442
Fat body of insects, 224, 227, 246
Fatty acids, 8, 442, 517
Feathers, 390, 533
Feather stars, 297
Feet. *See* Limb, hind, and Leg
Felidæ, 488
Felis, 488, 716
Female, 5
  gamete. *See* Gametes
Femur, **416.** *See* Bone, femur
Fenestra ovalis, 352, 426, 467
  rotunda, 426, 467
Fenestræ of cockroach, 229
Fertilisation, 5, 456, 632
  self-, 97, 121
  See also Reproduction
Fertilisation membrane, 633, 640
Ferungulata, 487
Fibres, 517, 518, 519, 520
Fibrin, 528
Fibrinogen, 528
Fibroblast, 507, *518*
Fibrocytes, 518
Fibrocartilage, 520
Fierasfer, 146, 627
Filaria bancrofti, 142, 147
  loa, 142
  perstans, 142, 147
Filoplumes, 393
Filter-chamber of crayfish, 203
Filum terminale, 380, 457
Fingers, 415
Fins of dogfish, 311, 314, 318
  of lancelet, 299
  unpaired, 311, 558
Fishes, 550, 551, 557
Fission, 2
  binary—
    in *Amœba*, 32
    in *Entamœba*, 61
    in *Euglena*, 37
    in *Hydra*, 98
    in *Paramecium*, 51
    in *Polytoma*, 35
    in *Trypanosoma*, 64
    in *Vorticella*, 57
  budding, 57n
  in Protozoa, 57n
  multiple, 42, 57n
  repeated, 35, 57n
Flagella, 20, 36, 39, **40,** 93, *505*, 632
Flagellata, 34, *78*
Flagellated chambers of sponges, 82
Flagellispores, 43
Flagellulæ, 43
Flagellum of snail, 269
Flame cells, 118, 304
Flatworms, 115
Flavinmononucleotide (FMN), 536
Flea, 145, 243, *259*, 485
Flight of cockroach, 223
  of pigeon, 394, **396, 397**
Flocculus, 460
Fluids of body, 508, *528*
Fluke, liver, 115. *See* Liver fluke
Fœtus, 672
Follicle of ovum, 456, 546, 676
Follicle-stimulating hormone, 676
Fontanelle, anterior, of dogfish, 315
  coracoid, 354
Fontanelles of skull, 350
Food and feeding, 7
  of *Ammocœtes*, 549
  of *Amœba*, 27
  of *Ascaris*, 135
  of cockroach, 218, 225
  of crayfish, 204
  of dogfish, 310, 323
  of earthworm, 161
  of *Entamœba*, 61
  of *Euglena*, 37
  of frog, 345, 364
  of *Hydra*, 94
  of lancelet, 303
  of leech, 181
  of liver fluke, 116
  of *Monocystis*, 41
  of *Paramecium*, 48
  of parasites, 145
  of *Peranema*, 38
  of plants, 18
  of *Polytoma*, 34
  of protoplasm, 18
  of rabbit, 414, 442
  of snail, 267
  of sponges, 82
  of starfish, 289
  of swan mussel, 275
Food chains, 21
Foot, 415. *See also* Limb, hind
  of *Hydra*, 87
  of molluscs, 264
Foramen, iliosciatic, 403
  interventriculare, 384
  intervertebral, 420
  lacerum anterius, 581

Foramen, magnum of dogfish, 316
of frog, 350
of pigeon, 399
of rabbit, 423
obturator, 403, 432
of Monro, 384, 616
of Panizza, 604
optic, 425, 581
triosseum, 402
vertebral, 419
Foramina of skull, in dog, 429
in dogfish, 316
in frog, 351
Foraminifera, 79
Fore-gut, 203. *See also* Stomodæum
Foreskin, 455
Forficula auricularia, 249
Formed material, 499
Formica rufa, 263
Fossa, mandibular, of frog, 354
ovalis, 446
pituitary, 581
Fossæ of reptiles, **583,** 584
Fossorial, 476, 495
Fovea, 413, 464, 540
Fowl, 595
Fox, 488
Frog, *344*, 555, 561, 598
alimentary system of, 360
arterial system of, **370**
blood vessels of, 369
brain of, 383
Ciliata in, 59
cleavage of ovum of, 649
cœlom of, 652
cranial nerves of, **381,** 384
development of, 649
ductless glands, 364
excretory organs of, 375, **629**
external features and body-wall of, 344
fat body of, **518**
hand of, **345**
heart of, 366
limb-girdles, 354
limbs, 356
locomotion of, 357
muscular system of, **358, 359**
nervous system of, 380, 653
reproductive organs of, 376
respiration of, 374
sense organs of, 385, **541**
skeleton of, 347
skin of, **345,** 347
skull of, 350, **579**
teeth of, 352, 353, **360**
vascular system of, 366
venous system of, **371**
Frog, vertebræ of, 348
Frons, 221
Frontal lobe, 458
Fructose, 116
Fruit-fly, 704
Fungi, 18, 259
Funiculi, 539
Fur, 414
Furcula, 402

Gadflies, 259
Gadus, 552
Galea, **222**
Gall-bladder, 438, 597
Gambia fever, 65
Gametes, 4
dimorphism of, 5
male and female, 5
maturation of, 700
of malaria parasite, 72, 75
of man, **3, 5**
of *Mastigophora*, 35
of *Monocystis*, 42
of *Paramecium*, 52
See also Ovum, Spermatozoon
Gametocyte, 72, 75
Gametogenesis, **547,** 702
Gamont, 72, 75
Ganglion, ganglia, 457
cerebral, of molluscs, 268, 280
cerebral. *See also* Suprapharyngeal and supraœsophageal
cerebro-pleural, 280
cervical sympathetic, 622
cœliac, 463
dorsal root, 380
Gasserian, 385
geniculate, 385
of cockroach, 228
parietosplanchnic, 281
pedal, 269, 281
pleural, 269, 281
pro-otic, 384
subœsophageal, of cockroach, 228
of crayfish, 211
of snail, 269
subpharyngeal, of earthworm, 165
supraœsophageal, of cockroach, 228
of crayfish, 210
suprapharyngeal, of earthworm, 165
sympathetic, 622
of frog, 385
of rabbit, 462
thoracic, of crayfish, 211
visceral, of molluscs, 269, 281

Gape, 360
Gärtner's canal, 631
Gastric mill of crayfish, 204
  ossicles, 204
Gastrin, 469
Gastroliths, 204
Gastropoda, 284
Gastrula, 636, 682
  of bird, 661
  of frog, 652
  of lancelet, 642
  of liver fluke, 122
  of starfish, 670
Gastrulation, 636
  of bird, 661
  of frog, 650
  of lancelet, 643
Gen e, 221
Gene complex, 709
Genera, 22, 716
Generative (or reproductive) organs,
  of *Ascaris*, 135
  of Chætopoda, **184**
  of cockroach, 229
  of crayfish, 215
  of dogfish, 333
  of earthworm, 171
  of frog, 376
  of *Hydra*, 96
  of lancelet, 307
  of leech, 182
  of liver fluke, 119
  of lizard, **631**
  of medusæ, 103
  of *Nereis*, 178
  of pigeon, 411
  of rabbit, 454
  of snail, 269
  of starfish, 293
  of swan mussel, 278
  of tapeworm, 126
Generic name, 22
Genes, 707
Genital organs. *See* Generative organs
  pouch of cockroach, 223
  rachis, 293
  stolon, 293
Genotype, 693
Gentles, 257
Geological record, 720
Gephyrea, 185
Germ cells, 5. *See also* Gametes
  layers, 186, 637
Germinal disc, 659. *See* Blastodisc
  vesicle, 641
  wall, 660
Giant fibres, 166
Gill bars, 302
Gill clefts. *See* Gill slits
Gill cover of crayfish, 195
  of fishes. *See* Operculum
Gill slits, 598
  of dogfish, 310, 323
  of lancelet, 299, 302, 645
  of tadpole, 654, 656
Gills, 598
  dermal, of starfish, 287
  external, 599, 656
  of crayfish, 208
  of dogfish, 323, **599**
  of mussel, 274
  of tadpole, 656
  -rays, 318
Girdle, limb, 565
  pectoral, or shoulder, 565
    of cod, **566**
    of dogfish, 318
    of duckmole, **497**
    of *Eogyrinus*, **567**
    of frog, 354
    of lizard, **567**
    of man, **568**
    of pigeon, 401
    of rabbit, 431
  pelvic or hip, 565
    of dogfish, 320
    of frog, 355
    of lizard, **568**
    of pigeon, 402
    of rabbit, 432
Gizzard of cockroach, 225
  of earthworm, 161
  of pigeon, 404, 596
Gland(s), 512
  adrenal, 16, 343, 366, 470
  albumen, 269
  antennary, 209
  buccal, 267
  carotid, 370, 609
  clitellar, 183
  colleterial, 229
  conglobate, 229
  Cowper's, 454 456
  ductless, 16, 513, 674
    of dogfish, 343
    of frog, 364
    of rabbit, 469
  grease. *See* Sebaceous
  green, 209, 680
  Harderian, 464
  infraorbital, 440
  interrenal, 343
  lacrimal, 464
  lime, 161
  lymph, 530

Gland(s), milk, 415, 512
mucous, 269
multicellular, **513**
mushroom-shaped, 229
œsophageal, 161
oil, 390, 533
parotid, 440
perineal, 415
pituitary, 311, 336, 347, 366, 411, 470, 674
prostate, 182, 454
racemose, **513**
rectal, 323
salivary, of cockroach, 225
of rabbit, 440
sebaceous, 512, 532
shell, of dogfish, 333
of liver fluke, 120
stink, 223
sublingual, 440
submaxillary, 440
suprarenal, 343
sweat, 452, 532
tear, 464
thoracic, of insects, 246
thyroid, 325, 347, 365, 469, 513
unicellular, **513**
yolk, 120
See also Liver, Pancreas, etc.
Glenoid cavity, 355, 431
facet, 318
Glires, 483
Glis glis, 485
Glochidium, 281
Glomeruli, of kidney, 453, 627
Glossa, **222,** 242
Glossina, 255
morsitans, 67
pallidipes, 67
palpalis, 66
submorsitans, **241**
swynnertoni, 67
tachinoides, 66
Glottis, of frog, 362
of rabbit, 437, 444
Glucagon, 470, 536
Glucose, 8, 9, 116, 453, 508
Glutamic acid, 535
Glutathione, 95
Glycerol, 8, 9, 442
Glycine, 8
Glycogen, 48, 132, 441, 471, 536
Glycolysis, 536
Gnathostomata, 550
Gnats, 72, 73, 142, 145, 239, **241,** 256, **257.** *See also* Mosquito
Golgi body, 502
Gonads,
See Ovaries, Testes
Gonangium, 104
Gonapophyses, 223
Gonepteryx rhamni, 255
Gonocœle, 307
Gonotheca, 104
Gonotome, 649, 665
Graafian follicles, 456, 546, 676
Grasshoppers, 248
Graviportal, 564
Grebes, 145
Green bodies of *Hydra viridis*, 93
Greenfly, 252
Green glands of crayfish, 209
Grey crescent, 649
matter, 384, 457, 458, 539, 616
Groove, cervical, 195
epipharyngeal, 303
oronasal, 310
primitive, 671
Ground substance, 508, 515
Growth, 1, 2, 4
changes in structure during, 4
Grylloblatta, 248
Grylloblattodea, 248
Gubernaculum, 454
Guillemot, 731
Guinea worm, 141, 150
Gullet of cockroach, 225
of crayfish, 203
of frog, 363
of pigeon, 403
of rabbit, 437
of snail, 267
of swan mussel, 275
of vertebrates, 596
See also Œsophagus
Gunda ulvæ, 129
Guppy, 657
Gut. *See* Canal, alimentary
Gymnophiona, 555, 627
Gymnospores, 43n

Haddock, **552**
Hæmocœle, 188
of cockroach, 224
of crayfish, 202
of snail, 268
of swan mussel, 275
Hæmocyanin, 207, 268
Hæmoglobin, 133, 163, 189, 451, 528, 708
Hæmopis, 185
Hagfish, 549
Hairs, 532
Haliclystus, 111
Hallux, 357, *415*

Halteres, 244
Hamster, cleavage of eggs of, **669**
Hand, 415. *See also* Limb, fore
of frog, **345**
Haploid, 702
Harderian glands, 464
Hare, 484
'Hare lip' of rabbit, 414
Hartmanella, 79
Harvestmen, 236
Hatching of lancelet, 645
Hatschek's pit, 301, 648
Haversian systems, 522
Head, 176, *192*, *573*
of cockroach, 221
of dogfish, 310
of frog, 344
segmentation of, 574
Heart, 602
of cockroach, 228
of cod, **604**
of crayfish, 204
of dogfish, 324
of frog, 366, 656
of pigeon, 407
of rabbit, 445
of reptiles, 604
of snail, 268
of swan mussel, 279
Heart-beat, 623
Hearts, lymph, 373, 530
Heat production, 12
Heat transport, 452
Hedgehog, 475, 476
Helicotrema, 467
Heliozoa, 79
Helix, 264. *See* Snail
aspersa and *pomatia*, 264, 269
Hemibranch, 322, 323, 598
Hemichordata, 308
Hemimetabola, 245
Hemiptera, 251
Hensen's node, 663, 671
Hepato-pancreas. *See* Digestive diverticula
Heptanchus, 576
Heredity, 4, *688*
Hermaphrodite duct, 269
Hermaphrodites, *6*, 52, 171, 182, 269
Hermaphroditism, 6, 152
Hermit crabs, 144
Heterocercal tail, 311, 314, 559
Heterochrony, 671, 673
Heterocœlous, 395
Heterodera, 140
Heterokaryota, 80
Heterometabola, 245
Heteronereis, 176, 178
Heterotype division, 702
Heterozygote, 689, 693
Hexapoda. *See* Insects
Hexoses, 441, 535
Hibernation, 476, 477
Higher organisms, 14
Hind-gut, 203. *See also* Proctodæum
Hippocampus, 459
Hippopotamus, 492
Hippospongia, 85
Hirudinea, 185
Hirudo medicinalis, 178, 185
Histiocyte, 518, 531
Histology, 506
Holoblastic cleavage, 636
Holocephali, 589
Holometabola, 245
Holonephros, 627
Holophytic, 38
Holothuria, 297
Holothuroidea, 297
Holozoic, 39
Homokaryota, 80
Homocercal, 559
Homoiothermic animals, 452
Homotype division, 702
Homo sapiens, 478. *See* Man
Homozygote, 689, 693
Hooke, R., 498
Hookworm, 140
Hooves, 533
Hormiphora plumosa, 114
Hormones, 16, 175, 189, 212, 220, 246, 364, *469*, 674, 686, 735
Horns, 492, 533
Horse-leech, 185
Horses, 490, **564**
feet of, **490, 720**
Host, 145, 147, 153. *See also* Parasites; Parasitism
House-flies, 240, **241,** 257
Hover flies, 259
Humerals, 391
Humour, aqueous, 464, 625
vitreous, 464, 625
Hybridisation, 733
Hydatid cyst, 130
Hydra, 86, 107, 144
buds of, 98
development of, 97
food of, 94
histology of, **89**
movements of, 94
nervous system of, 90, **91, 92**
regeneration of, 98
reproduction of, 96
Hydra attenuata, 86, 96
oligactis (=*fusca*), 86, 96

Hydra viridis, 86, 96
Hydranths, 101
Hydrochloric acid, 441
Hydrogen acceptors, 10, 536
 ion concentration, 189
Hydroids, 99
Hydrolysis, 9
Hydrorhiza, 101
Hydrotheca, 101
Hydrozoa, 108
Hymenoptera, 260
Hyoid apparatus, of frog, 354
 arch in skeleton of dogfish, 316
 of pigeon, 401
 of rabbit, 430
Hyostylic, 589
Hypapophysis, 422
Hypermetamorphosis, 245, 260
Hyperphalangy, 565
Hypoblast, 186, 637, 660, 670
Hypocercal, 559
Hypoderma, 145
Hypodermis, 132
Hypohippus, **720**
Hypomere, 648
Hypopharynx of cockroach, **222**, 225
 of insects, 239
 of mosquito, 239
Hypophysis, 384, 470, 580
Hypostome (oral cone), 87
Hypothalamus, 674
Hyracoidea, 491
Hyracotherium, **720**

Ichneumon flies, 147, 260
Ichthyopterygium, 561
Ichthyosauria, 560, **561**
Ileum of cockroach, 225
 of frog, 363
 of pigeon, 405
 of rabbit, 438
Iliosciatic foramen in the pigeon, 403
Ilium, 356, 402, 432, 567
Imago, 244
Immunity, 148
Inclusions, 501
Incorporation of food, 7
Incus, 426, 594
Individuality, 105
Induction, 640, 665
Infundibulum, 384, 618
 of rabbit, 444, 460
Inguinal canal, 454
Inhalant canals of sponges, 82
Inheritance of acquired characters, 734
Inner cell mass, 668
Insecta, 237
Insectivora, *475*, 488
Insects, 237, 681
 life-history of, 244
 mouth-parts, 237
 wings, 243
Insertion, of muscle, 419, 545
Instar, 244
Instep, 415. *See* Metatarsus
Instincts, 412, 618
Insulin, 470, 536
Intercalary pieces, 315
Intercellular substance. *See* Ground substance
Interclavicle, 402, 568
Intermediate cell mass, 665
Internal environment, 189
Interoceptive, 619
Interradius, 287
Interrenal body, 343
Interstitial cells, 88
Intervertebral discs, 520
 notches, 420
Intestine—
 histology of, 533
 structure of, **13**
  in vertebrates, 595
 See also Canal, alimentary
Invertebrates, development of, 676
In vitro, 506
In vivo, 506
Ions, as food, 7
Iris, 464, 624
Irritability, 2, 7
 in *Amœba*, 27
Ischiopodite, **197**
Islets of Langerhans, 469, 513, 537
Isogamy, 35
Isolation, 730
Isopoda, 234
Isoptera, 249
Itch, 236
Iter, 337, 616
Ivory, 436
Ixodes, **238**

Jacobson's anastomosis, 385
Jaw, lower, 591. *See* Mandible,
  upper, 587. *See* Skull
Jaws of dog, 426
 of dogfish, 316
 of frog, 353
 of Vertebrata, 587
 suspension of, 316, *588*
Jelly-fish, 109

Jerboas, 485
Joints, **418**, 545
Juice, gastric, 11

Kala-azar, 66
Kangaroos, 495
Kappa, 713
Karyogamy, 6
Karyokinesis, 696
Karyosome, 63
Katabolism, 12
Keber's organs, 279
Keel, 402
Keilin, D., 145
Keratin, 132, 311, 486, 507, 510, 511, 532
Kerona, 144
a-ketoglutaric acid, 535
Kidneys, 545, 626
  of dogfish, 329
  of frog, 375
  of pigeon, 410
  of rabbit, 453
  of snail, 268
  of swan mussel, 278
Killer, 713
Killer whale, **487**
Kinetism, 589
Kinetodesma, 47
Kinetoplast, 64, 502
Kinetosome, 39
Kiwi, 412
Knee-cap, 435

Labellum, 240, 242
Labial palp of cockroach, **222**
Labium of cockroach, **222**, 225
  of other insects, 239, 243
  of mussel, 274
Labrum of cockroach, 221
  of crayfish, 202
  of Diptera, **241**
  of hemipteran, **240**
  of insects, 238
Labyrinth—
  auditory, of dogfish, 342
    of frog, 386
    of pigeon, 412
    of rabbit, 467
    of vertebrates, 626
  carotid, 370, 609
Lacerta, 556, 604. *See* Lizard
Lacewings, 253
Lacinia, **222**
Lactic acid, 471
Lacunæ of bone, 521
Lagena, 386
Lagomorpha, 483, *484*
Lamarck, J. B. de, 734
Lamella, structureless. *See* Mesogloea
Lamellæ of bone, 521
  of gills of mussel, 274
Lamellibranchiata, 284
Lamina terminalis, 384, 616
Lampetra fluviatilis, 549
Lamprey, 548, 549, 559
Lancelet, *298*, 308, 557, 558
  alimentary system of, 301
  atrium of, 299
  development of, 636, *640*
  external features and habits of, 298
  larva of, 645
  nephridia, 304
  nervous system of, 306
  reproductive organs of, 307
  respiration of, 306
  sense organs of, 306
  sperm of, 633
  vascular system of, 305
Large intestine, 439
Larva, 136, *244*, 245, 379
  apodous, 245
  campodeiform, 245
  eruciform, 245
  of frog, 656
  of lancelet, 645
  oligopod, 245
  polypod, 245
  See also Ammocœte, Bipinnaria, Brachiolaria, Glochidium, Planula, Tadpole, Trochosphere
Larval excretory organ, 627
Larynx, 374, 405, 444
Latent bodies of trypanosomes, 66
Lateral, 187
Lateral fin-fold theory, 560
Lateral line of dogfish, 342
  plate, **571**, 574
Latimeria, 553, **722**
Latin names, 22, 716
Laurer-Stieda canal, 120
Law of Mass Action, 529
Layers, germ, 186, 645
Learning, 412
Leather-jackets, 259
Lebistes, 657
Le Chatelier's principle, 735
Lecithins, 632
Lecky, W. E. H., 718
Leech, medicinal, 178
Leeches, 150, 185
Legs of Arachnida, 235
  of cockroach, 222
  of crayfish, 198

Legs of primates, **725**
See also Limb
Leishmania, 66
Lens of eye, 342, 464, 624
Lepas, 235
Lepidoptera, 253
Lepidosauria, 586, 613
Lepidosiren, 546, 599, 600, 604
Lepidosteus, 600
Lepisma saccharina, 247
Lepus, 414. *See also* Rabbit
Lepus europæus, 484
Lepus timidus, 484
Leucilla, 83
Leucocytes, 529
Leucon, 84
Lice. *See* Louse
Life, characteristic features of, 1
Life, cycle of, 4
Life-history of *Ascaris*, 136
of *Aurelia*, 109
of *Entamœba*, 61
of frog, 656
of house-fly, 258
of insects, 244
of liver fluke, 122
of malaria parasite, 68, **74**
of *Monocystis*, 42
of mosquito and gnat, **257**
of Nematoda, 138
of *Nereis*, 178
of *Obelia*, 103
of *Opalina*, 104
of sea-anemone, 112
of starfish, 293
of swan mussel, 281
of tapeworm, 126
of *Trypanosoma*, 64
See also Reproduction, Development, Embryology
Ligament, 519
broad, 630
ethmopalatine, 316
falciform, 438, 597
hepatoenteric, 596, 597
postspiracular, 316
suspensory, 323
Ligamentum nuchæ, 519
Light, effects of, 674
production of, 12
Limb, biramous, 197
fore, of *Balænoptera*, **486**
of dogfish, 318
of frog, 356
of man, **435**
of pigeon, 401
of rabbit, 415, 434
Limb, hind, of dogfish, 320
Limb, hind, of frog, 357
of pigeon, 402
of rabbit, 415, 435
pentadactyl, **416,** 561
Limbs. *See* Legs, Appendages
of backboned animals, 560
position of, 569
Limnæa stagnalis, 122
truncatula, 122
Limpet, 284
Lingua, 239
Linkage, 703
Linnæus, C., 716
Lipase, 442
Lips, 435
Liver, 531, 534, 597
function of, 535
of crayfish, 204
of dogfish, 323
of frog, 363
of pigeon, 405
of rabbit, 438
Liver fluke, 115
excretory system, 118
nervous system, 119
reproduction, 119
Liver rot, 115
Living and lifeless things, 1
Living matter, structure of, 12
Lizard, the, 555, 556
arteries of, **613**
pelvic girdle of, **568**
shoulder girdle of, **567**
skull of, **588**
urinary and genital organs of, 631
viscera of, 630
Loa loa, 142
Lobster, 234, **633**
Lobi inferiores, 336
Locomotion of *Amœba*, 26
of *Asterias*, 294
of *Euglena*, 36
of *Hydra*, 94
of medusæ, 102
of *Paramecium*, 46, 49
of cockroach, 223
of crayfish, 200
of dogfish, 312
of earthworm, 166, **169, 170**
of frog, 357
of leech, 179
of pigeon, 394
of snail, 264
of swan mussel, 273
Læmanctus longipes, **567**
Loop of Henle, 453
Lophodont teeth, 484, 495

Louse, 145, 243, 244, *250*
Love dart of snails, 269
Lower jaw. *See* Mandible
  organisms, 14
Lucernaria, 111
Lugworm, 185
Lumbar vertebræ, 422
Lumbricus terrestris, 155, 156, 175, 185
  See also Earthworm
Lung-books, 235, **236**
  -fishes, 552, 559
Lungs, 519, 537, 599
  of frog, 374
  of pigeon, **406,** 407
  of rabbit, 444, **600**
Luteinising hormone, 676
Luteotropic hormone, 676
Lutra lutra, 489
Lymph, 373, 452, 530
  glands, 530
  hearts, 373, 530
  nodes, 530
  sacs, 347
Lymph system, 530
  human, **451**
Lymphatic vessels of frog, 373
  of lancelet, 305
  of rabbits, 452
Lymphocyte, 531
Lymphoid tissue, 531
Lysins, 149
Lysosome, 502

Macrogametes, 75
Macromere, 677
Macrophage, 518
Macropus, 495
Macula, 385
Madreporite, 288, 291
Maggots, 257
Malacostraca, 234
Malaria parasites, *68*, 147. *See Plasmodium*
  terminology of, 75
Male, 6
  gamete. *See* Gametes
Malleus, 426, 428, 594
Mallophaga, 150, *250*
Malpighian body, 453
  layer of skin, 510
  tubules of cockroach, 225, 227
Malthus, T. R., 728
Maltose, 8, 441
Mammæ, 415, 482
Mammalia, *474*, 557, 584
  development of, 673
Man, 458, 464, *478*, 519, 532, 582, 595, 615, 681, 702, 712
  alimentary canal of, **481, 482**
  arm of, **435**
  blood of, 528
  bones of hind limb of, compared with other mammals, **564**
  coccyx of, **480**
  ear of, **726**
  lymphatic system of, **451,** 530
  palate of, **483**
  shoulder girdle of, **508**
  skull of, **479**
  sperm of, **5, 633**
  spinal cord of, **538**
  uterus of, **482**
  vas deferens of, **482**
Mandible of cockroach, **222,** 225
  of crayfish, 198
  of dogfish, 316
  of *Eogyrinus*, **591**
  of frog, 353
  of insects, 237
  of pigeon, 401
  of rabbit, 428
  of vertebrates, 591
Mandibular arch. *See* Arches, visceral
  fossa, 354
Maniola jurtina, 255, 731
Mantle of molluscs, 266, 271
Manubrium of medusa, 101
  sterni, 423
Manus, 415
Marrow, 521, 531
Marsupialia, 494, 673
Marsupium, 495
Marten, 489
Manyplies, **493**
Martes martes, 489
Mastigophora, 77
Mastoid process, 425
Maturation of gametes, 632, 702
Maxillæ of cockroach, **222,** 225
  of crayfish, **196,** 198
  of insects, 237
  of vertebrates, 353, 401, 427, 591
Maxillary palp of cockroach, 222
  of mosquito, 240
Maxilliped, **196,** 198
Maxillopalatine process, 401
Maxillule, **196,** 198
Mayfly, 245, *248*
'Measly' pork, 127
Mechanical tissue, 508, 515
Mechanocyte, 507
Meckel's cartilage, 316, 353, 428, 587
Mecoptera, 253

Medial, 187
Mediastinum, 418
Medulla of adrenal bodies, 366
of green glands, 210
of kidney, 545
oblongata of dogfish, 337
of frog, 383
of rabbit, 460
Medullary plate. *See* Neural plate
sheath, 515
Medusæ, 101, **108**
Meganucleus, 48, 54
of *Paramecium*, 48, 54
of *Vorticella*, 56
Meiosis, 53, 700
Melanin, 532
Melanocytes, 511, 532
Melanophores, 366
Meles meles, 489
Membrana granulosa, 546
semilunaris of pigeon, 407
Membrane bones, 523, 565, 582
Membranes, 12
Membrane(s) double, 501
embryonic, 663
periodontal, 437
peritrophic of cockroach, 226
Mendel, Gregor Johann, 688
Meninges, 538
Mentum of insects, 239
Merism, 106
Mermaids' purses, 334
Mermis nigrescens, 141
Meropodite, **196**
Merozoite, 75
Mesencephalon, 616
Mesenchyme, 655
Mesenteries of sea-anemones, 111
Mesenteron (midgut) of *Ascaris*, 134
of cockroach, 225
of crayfish, 204
of frog embryo, 654
Mesentery, 417, 655
Mesoblast, 186, 637, 655
Mesoblastic somites. *See* Somites
Mesoderm, 107, 186, 191, 637. *See also* Mesoblast
of chick, 662
of frog, 651, 655
of lancelet, 644
Mesogloea, 87, 107, 109
Mesohippus, **720**
Mesonephros, 627
Mesopterygium, 320
Mesorchium, 376
Mesosoma, 236
Mesothelium, 534
Mesothorax, 221
Mesovarium, 377
Metabolism, 11
Metacarpal quills, 391
Metacarpus, 357, 402, 415
Metacercaria, 123
Metacromion, 431
Metagenesis, *105*, 130
Metameric segmentation, 191
Metamorphosis of insects, 244, 245
of lancelet, 645
of starfish, 294
of tadpole, 656
Metanephros, 629
Metaphase, 696, 702
Metapleural fold, 299
Metapodials, **416,** 492
Metapophysis, 422
Metapterygium, 320
Metasoma, 236
Metastome, 203
Metatarsus, 357, 403, 415
Metatheria, 495
Metathorax, 221
Metazoa, 77
Metencephalon, 616
Metridium, 112
Mice, 485
Microcheiroptera, 478
Microgametes, 75
Micromere, 677
Micromys, 485
Micronucleus of *Paramecium*, 48
of *Vorticella*, 56
Microphagy, 303, 486, 598
Microtinæ, 485
Microtus agrestis, 485
Midges, 259
Midgut. *See* Mesenteron
Midriff, 417
Milk, 415, 474
pigeon's, 411
Mill, gastric, 204
Millipedes, 237
Miner's worm, 140
Miracidium, 122
Mites, 236
Mitochondria, 29, 79, *501*, 515, 536, 632
Mitosis, 698
in *Amœba*, 32
in *Paramecium*, 51
Mitral valve, 446
Mole, 476
Molge, 554
Mollusca, 264, *283*, 610
Monimostyly, 589
Monkey, **564,** 673
Monorchus, 138

Monocystis, *41*, 79
  agilis, *magna* and *lumbrici*, 41
  life-history of, **44**
Monosiga, **39**
Monotremata, *496*, 585, 668
Morgan, T. H., 704
Morphogenesis, 106, 636
Morphology, 21
Morula, 636, 668
Mosaic image, 212
Mosquitoes, **73,** 256. *See* Gnats
  life history of, **257**
  mouth parts of, **241, 258**
Motacilla, 717
Moths, **242,** *253*
Moulting, of crayfish, 200
  of insects, 219, 246
Mouse, 485, 673
Mouth, 435, 511, 595. *See also* Canal, alimentary
Mucron, 42
Mucus, 264, 512
Mud-puppy, 555
Müllerian duct, 629, 631
Multiple fission, 43n, 69
Murinæ, 485
Mus, 485
Musca domestica, 240, **256,** 257
Muscardinus avellanarius, 485
Muscle, 508, *523*, 545
Muscle, extensor and flexor, 200
  fibres, 523
  insertion of, 419, 545
  origin of, 419, 545
  -plate, 648
  spindles, 526
Muscle or muscles specified—
  alary, 228
  biceps femoris, 382
  columella, of snail, 266
  eyeball, 342
  gluteal, 479
  intercostal, 444
  obliquus inferior, of eyeball, 342
    superior, of eyeball, 342
  of crayfish, 200
  of dogfish, 312
  of eathworm, 158
  of frog, **358,** 359
  of lancelet, 301
  of pigeon, 403
  of swan mussel, 271, 273
  pectoralis, 403
  protractor, of mussel, 271, 273
  protractor lentis, 385
  rectus externus or posterior of eyeball, 342
    inferior, of eyeball, 342
Muscle or muscles specified—
    internus or anterior of eyeball, 342
    superior of eyeball, 342
  retractor bulbi, 384
  retractor of mussel, 271, 273
    of starfish, 291
  semimembranosus, 382
Muscular tissue, 523
    cardiac, 527
    involuntary, 526
    of *Ascaris*, 132
    of earthworm, 158
    plain, 526
    skeletal, 523
    smooth, 526
    somatic, 523
    striated, 523
    striped, 523
    unstriped, 526
    visceral, 526
    voluntary, 523
Musculo-epithelial cells, 87
Mussel, swan, *270*, 284
  anatomy and alimentary system of, 275
  excretory organs of, 278
  external features of, 273
  feeding of, 273
  gills of, 274
  gonads of, 279
  life-history of, 281
  locomotion of, 273
  mantle of, 271
  nervous system of, 280
  sense organs of, 281
  shell of, 271
  vascular system of, 279
Mussels, freshwater, 270
Mustela, 489
Mustelidæ, 489
Mutants, 729
Mutation, 729
Mutica, 486
Myelencephalon, 616
Myelin, 515
Myocœle, 648
Myocommata of chick, 665
  of lancelet, 299
  of dogfish, 312
Myoepithelial cells. *See* Musculo-epithelial
Myofibrils, 524
Myohæmoglobin, 525
Myomeres of lancelet, 299, 648
  of dogfish, 312
Myonemes, 41, 56
Myosin, 524

Myotome, 570, 648, 665
Myriapoda, 237
Myxine glutinosa, 549

Nacreous layer, 266
Naiads, 245
Nails, 533
Nais, **184,** 185
Names, Latin, 22
Nares, external, of dogfish, 310
of dog, 428
of frog, 345
of pigeon, 390
internal, of Choanichthyes, 552
of frog, 360
of pigeon, 403
of rabbit, 435, 437
posterior. *See* Nares, internal
Narial passage, 437
Nasal capsules, 316, 352, 401, 423, 426, 579, 580, 584, 587
septum, 423, 435, 579
Nasopharynx, 436
Natrix natrix, 556, **586**
Natural selection, 728
Nauplius, 234
Nautilus, 285
Navel, 672
Neck of rabbit, 421, **463**
Necturus, 555
Nematocyst, 88, 89
Nematocystis, 41
Nematoda, *131*, 638
and Arthropoda, resemblances between, 142
life-histories of, 138
Neoceratodus, 552
Neognathæ, 556
Neopallium, 459, 618
Nepa, 251
Nephridia, 188
of earthworm, **162,** 163
of lancelet, 304
of leech, 181
Nephridiopores, 157, 163
Nephridiostome, **162,** 163
Nephrocœle, 627
Nephrocœlomostome, 627
Nephromixium, 188
Nephrostome, 627
Nephrotome, 570, 627, 665
Nereis, 175
cultrifera, 175, **176**
diversicolor, 193
Nerve, abducent, 340, 384
acoustic. *See* auditory
antennary, of cockroach, 228
anterior laryngeal, 462
Nerve, auditory, 341, 468, 575, 626
brachial, 382
buccal, 341
depressor, 462, 482
external mandibular, 341, 384
facial, 341, 384, 462, 620
glossopharyngeal, 341, 385, 462, 620
hyomandibular, 341
hypoglossal, 341, 382, 385, 462
laryngeal, 385, 462
lateral line, 341
mandibular, 341
maxillary, 341
oculomotor, 340
olfactory, 340, 462, 575
ophthalmic, 340, 341
optic, 340, 462, 464, 575, 625
of cockroach, 228
palatine, 341
pathetic, 340
pharyngeal, 462
phrenic, 462
pneumogastric. *See* Vagus
postspiracular,341
post-trematic, 341
prespiracular, 341
pretrematic, 341
profundus, 340
radial, 288
recurrent laryngeal, 462
sacral, 462
sciatic, 382, 462
spinal accessory, 341, 385, 462, 575
superficial ophthalmic, 340, 341
terminal, 340
trigeminal, 340, 384
trochlear, 340
vagus, 341, 385, 462, 620
Nerves, 538
composition of, 457, 619
cranial, *340*, 384, 412, 461, 577, 619
motor (efferent), 457, 619
sensory (afferent), 457, 619
somatic, 619
spinal, 337, 382, 462, 619
sympathetic. *See* Sympathetic system
visceral, 619
Nerve-components, **620**
-cord of cockroach, 228
of crayfish, 210
of earthworm, 165
of lancelet, 300, 306
of vertebrates. *See* Spinal cord
-cords of *Ascaris*, 134

Nerve-cords of liver fluke, 119
of starfish, 288
of *Tænia*, 126
-endings, **523, 526, 541**
fibres, 457, *515*
-muscle junction, 525, 621
net, 91, 128, 288, 296
rings of medusa, 103
Nervous impulses, 620
system, 16, 615
autonomic, 385, 457, 462, *621*
formation of, in vertebrates, 665
of *Ascaris*, 133
of cockroach, 228
of crayfish, 210
of dogfish, 335
of earthworm, 165
of frog, **379,** 380
of *Hydra*, 90
of lancelet, 306
of leech, 182
of liver fluke, 119
of medusæ, 103
of pigeon, 412
of rabbit, 457
of snail, 268
of starfish, 288
of swan mussel, 280
of tapeworm, 126
sympathetic, *see* autonomic
tissue, 508, *514*
Nervures, 222
Neural arch, 419
crest, 654, 655, 666
folds, 653
(medullary) plate, 623, 643, 653, 661
groove, 653
spine, 419
tube, 662
vessels of earthworm, 165
Neurilemma, **516**
Neurocyte, 508
Neurofibrils, 515
Neuroglia, 515
Neurohumours, 471
Neuromast organs, 342
Neuron, 514
Neuropodium, 176
Neuropore, 644, 654
Neuroptera, 253
Neurula, 654
Newton's second law, 735
Newts, 554
Nicotinamide, 10
Nictitating membrane, 385
Nipple, 532
Nitrogenous waste, 8. *See also* Excretion
Nodes of Ranvier, 515
Nomina conservanda, 716
Non-cellular animals, 76
Non-disjunction, 706
Nostrils. *See* Nares, external
Notidani, 589
Notochord of chick, 661, 663
of dogfish, 314
of frog, 349, 650
of lancelet, 301, 643, 644
of rabbit, 671
Notonecta, 251
Notopodium, 176
Notum, 221
Nuclear division, 696
membrane, 503
Nucleic acid, 503, 707
Nucleoplasm, 499 *503*
Nucleus, 13, *498*, 503
Nutrition, holozic, holophytic, saprophytic, 38
of *Amœba*, 27
of *Paramecium*, 48. *See also* Food
Nuthatch, 730
Nyctotherus, 59
Nymph, 136n, 244

Obelia, 99, 109
hydranth of, **100**
medusa of, **101, 102, 103**
reproduction of, 103
Obturator foramen, 403, 432
Ocelli, 245
Occipital condyles, 350, 423. *See also* Skull
Octopus, 192, 285
Odonata, 248
Odontoid process, 421, 573
Oesophageal pouches, 161
Oesophagus,
of dogfish, 322
of earthworm, 160
of frog, 363
See also gullet
Oestridæ, 259
Oestrogen, 676
Oestrus, 456, 676
Offspring, 3
Olecranon, 356, **433**
Olfactory bulb and tract, 459
capsules. *See* Nasal capsules
lobes, 336, 384, 412, 459, 616
membrane, 540
organs of cockroach, 214
of crayfish, 229
of dogfish, 342

Olfactory organs of frog 388
of pigeon, 412
of rabbit, 468
of snail, 269
of snake, 595
of swan mussel, 281
pit, 306
Oligochæta, 185
Olynthus, 81, **82, 83**
Omentum, 323, *417*
Ommatidia, 212
Omosternum, 355, 569
Oncosphere, 127
Onychophora, 237
Oocyst, 75
Oocytes of *Hydra*, 97
Oogamy, 35
Oogenesis, 702
Ookinete, 75
Ootheca, 230
Opalina, 80
ranarum, 59
Open circulatory system, 188
Operculum,
of fishes, 551
of nematocyst, 88
of snails, 266
of tadpole, 657
Ophiothrix, 296
Ophiuroidea, 296
Opisthosoma, 236
Opossums, 496
Opsonins, 149
Optic chiasma, 342
cup, 623
lobes, 337, 383, 412, 460
thalami, 384, 460
Oral cone of *Hydra*, 87
of *Obelia*, 101
hood, 298, 301
Orbit of dogfish, 315
of dog, 425
of pigeon, 399
Orca gladiator, **487**
Order, *22*, 717
Organic compounds, 7
evolution, 718
Organisation, 13
Organiser, 640, 653, 662, 683
Organism, 14
Organs, *13*, 531
vestigial, 726
Origin of muscle, 419, 545
Origin of Species, 718
Ornithodorus moubata, 236
Ornithorhynchus, *496*, 585
Orohippus, **720**
Oronasal groove, 310
Orthoptera, 248
Oryctolagus cuniculus, 414. *See* Rabbit
Os coxæ, 432
innominatum, 432, 569
Osculum, 81
Osmosis, 193, 452
Osmotic pressure, 29, *192*, 227
regulation, 210, 333
Osphradium, 281
Ossicles, auditory, 426, 428, 594
of crayfish, 204
of starfish, 287, 288
Osteichthyes, 551, 560, 566
Osteoclast, 522
Osteocytes, 521
Ostia of cockroach, 228
of crayfish, 204
of sponges, 82
Ostracoda, 234
Ostracoderms, 559
Ostriches, 556
Otter, 489
Ovaries of *Ascaris*, 135
of cockroach, 229
of crayfish, 215
of earthworm, 171, **173**
of frog, 376
of *Hydra*, 96
of leech, 182
of liver fluke, 119
of lizard, 631
of mammal, 546, 676
of rabbit, 456
Ovary of dogfish, 333
of pigeon, 411
Oviducts of *Ascaris*, 136
of cockroach, 229
of crayfish, 215
of dogfish, 333
of earthworm, 172
of frog, 377
of leech, 183
of liver fluke, 119
of lizard, 631
of pigeon, 411
of rabbit, 456
of snail, 269
of Vertebrata, 630, 687
Ovipositor, 260
Ovotestis, 269
Ovoviviparous, 657
Ovulation, 456, 676
Ovum, 5, 632
maturation of, 632, 702
of birds, 411, 659
of crayfish, 216
of dogfish, 333

Ovum of frog, 649
of hamster, **669**
of lancelet, 640
of mammals, 668
of man, **3**
segmentation of, 636. *See* Cleavage
See also Reproduction
Ox, foot of, bones of, **493**
Oxygen, 8, 10, 18, 452
Oxyuris, **142**

Pachytene stage, 700
Pain, 463
Palæontology, 720
Palate, 435, 475
false, 427, 595
hard, 435
soft, 435
Palatopterygoquadrate bar, 426
Pallial line, 271
Pallium, 384, 458
Palm, 415. *See* Metacarpus
Palps of *Nereis*, 176
labial and maxillary, of cockroach, 221, **222**
labial, of mussel, 274
maxillary, of gnat, 240
Pancreas, 536, 597
of dogfish, 323
Pancreas of frog, 363
of man, **481**
of pigeon, 405
of rabbit, 438, 441, 469
Pancreozymin, 469
Panniculus adiposus, 519
Panorpa communis, 253
Pantothenic acid, 536
Papilla, urinary, 333
urogenital, 333
Parachordal plates, 577, 579
Paradidymis, **628**
Paragaster of sponge, 81
Paraglossa of cockroach, **222**
Paraglycogen, 41
Paragnatha, 202
Paramecium, 45
aurelia, 48
caudatum, **45**, 48, 51
conjugation in, 51
inheritance in, 713
locomotion, 46, 49
nutrition of, 48
reactions of, 49
reproduction in, 51
Paramylum, 36
Paraphysis, 618
Parapineal body, 618
Parapodia, 176
Paraprocts, 223
Parapsid, 585
Parasites, 144
ciliate, of frog, 59
effects on hosts, 147
protozoan, of man, 61
respiration of, 151
See also Acarina, Aphaniptera, Glochidium, Hemiptera, Nematoda, Platyhelminthes, and individual animals
Parasitic castration, 148
Parasitism, 144
Parasympathetic system, 527, 622
Parazoa, 85
Parenchyma of liver fluke, 116
of tapeworm, 126
Parent, 3
Parietal body, 618
lobe, 458
vessels of earthworm, 164
Paroophoron, **628**, 631
Parrot, 401, 478, 565, 589, 595
Pars intercerebralis, 246
Parthenogenesis, 6, 122, 231, 252, 262
Patella, 284
Patella, 435
Paunch, **493**
Paurometabola, 244
Pea, 688
Pearls, 272
Pecten in pigeon's eye, 412
Pectineal process, 403
Pectoral girdle. *See* Girdle
Pedicellariæ, 288, 295
Pediculus, 145, 250
Pedipalp, 235
Pellicle of *Euglena*, 36
of *Paramecium*, 47
Pelomyxa, 33
Pelvic girdle. *See* Girdle
Pelvis, 432
Penguins, 556
Penial setæ of *Ascaris*, 132
Penis of birds, 411
of leech, 182
of liver fluke, 119
of marsupials, 495
of rabbit, 415, 454, 532, 544
of snail, 269
Pentadactyl limbs, **416**, 561
Peppered moth, 719
Pepsin, 364, 441
Pepsinogen, 441
Peptone, 441
Peranema, 38

Pericardio-peritoneal canal, 320
Pericardium or pericardial cavity, 519, 655
of cockroach, 224
of crayfish, 204
of dogfish, 320
of frog, 366
of rabbit, 417
of snail, 268
of swan mussel, 275
Perichondrium, 520
Perihæmal cavity, 292
Perilymph, 386, 467
Periophthalmus, 687
Periosteum, 522
Periostracum, 266
Peripatopsis, 237
Peripatus, 237
Periplaneta americana, *218*, 230
australasiæ, 218
See also Cockroach
Perisarc, 101
Perissodactyla, 490, 563
Peristalsis, 166, 534
Peristome of starfish, 287
of *Vorticella*, 55
Peristomium of earthworm, 156, 167
of *Nereis*, 176
Peritoneal cavity, 655
of dogfish, 320
of rabbit, 417
funnel, 329, 627
Peritoneum, 655
Peritrophic membrane, 226
Perivisceral cavity of *Ascaris*, 132. *See also* Cœlom and Hæmocœle
Perla, 248
Pernicious malaria, 69
Pes, 415
Petrobius maritimus, 247
Phagocytes, 134, 149, 190, 246, 530
Phalanges, 357, 403, 415
Phalangida, 236
Pharynx of *Ascaris*, 134
of dogfish, 322, 342
of earthworm, 158, 160, 167
of frog, 362
of lancelet, 301
of leech, 181
of liver fluke, 115
of *Nereis*, 177
of rabbit, 435
of vertebrates, 595
Phasmida, 249
Phenotype, 693
Phobotaxis, 50
Phoca, 489
Phocæna, 487
Phosphate, 454, 505, 528
Photosynthesis, 18
Phthirus pubis, 145, 250
Phyllopodium, 197, 234
Phylum, 22, 717
Physalia, 109
Physiological division of labour, 14
Physiology, 21
Phytomastigina, 78
Pia mater, 383, 538
Pieces, intercalary, 315
Pieris brassicæ, 255
Pig, fore-leg of, **493**
Pigeon, 389
alimentary system of, 403
blood vessels of, 407
digestion in, 405
excretory organs of, 410
external features of, 389
feathers of, 390
flight of, 394
limbs of, 401
nervous system of, 412
reproductive organs of, 411
respiratory organs of, 405
sense organs of, 412
skeleton of, 395
skull of, 399
wing of, **389**
Pigment cells of eye of crayfish, 212
of retina, 540
of skin of frog, 347
of skin of mammals, **511**, 532
spot of *Euglena*, 37
of *Polytoma*, 34
Pigs, 492
Pinacocytes, 81
Pineal body or organ, 618
of frog, 384
of rabbit, 460
stalk in dogfish, 336
Pinna, 414, 521
Pinocytosis, 27
Pipistrellus pipistrellus, 478
Pisces, 550
Pisum sativum, 688
Pituitary body, 618
function of hormones of, 311, 347, 411, 470
of dogfish, 336
of frog, 366, 384
of rabbit, 423, 460
Placenta, 456, 671, 674
Placentalia, 474

Placodermi, 550, 558
Placoid scales, 312
Plague, 260
Planaria, 129
Plantar surface, 415
Plantigrade, 416, 476, 479, 483, 489
Plants, differences between animals and, 16
Planula of *Aurelia*, 109
of *Obelia*, 104
of sea-anemones, 112
Plasma of blood, 528
Plasmagel, 26
Plasmagenes, 713
Plasmalemma, 24, 27
Plasmasol, 26
Plasmodium, 68, 79, 147, 152
life-cycle of, **74**
falciparum, 68
malariæ, 68, 153
ovale, 68
vivax, 68, 149, 153
Plasmogamy, 6
Plastogamy, 33
Plate, cribriform, 423, 580
epicranial, 221
lateral, **571**, 574
muscle, 648
neural or medullary, 623, 661
Plates, podical, 223
pole of *Paramecium*, 51
Platybasic, 580
Platyhelminthes, 115, *128*
Platypus, 496
Plecoptera, 248
Plecotus auritus, 478
Pleiotropism, 703
Pleura of crayfish, 194
of cockroach, 221
Pleuræ of rabbit, 418
Pleural cavities, 417
Pleurobranchiæ, 209
Pleuroperitoneal cavity. *See* Cœlom
Plexus, anterior choroid, 384, 618
Auerbach's, 533, 623
brachial, 382, 462
hepatic, of lancelet, 305
lumbosacral, 462
Meissner's, 533, 623
nephridial, of lancelet, 305
posterior choroid, 383, 618
sciatic, 382
solar, 463
sympathetic, 527
Podical plates, 223
Podobranchia, 209
Podomeres, 221
Podophyra, **79**
Polar bodies, 632, 702
lobe, 676
Polecat, 489
Pole capsules, 76
cells, 679
plates, 51
Poles of egg, 634
Pollex, 415
Polychæta, *183*, 676
Polycelis nigra, 129
Polygenes, 708
Polymorphonuclear cells, 529
Polyœca, **39**
Polyp, 87
of *Obelia*, 100
See also Hydra, Sea-anemones
Polyphenol layer, 220
Polyphyodont, 322
Polyploidy, 733
Polypterus, 566, 599, 600
Polyspermy, 657
Polytoma, *34*, 78
uvella, **34**
Pomatoceros, 676
Pons Varolii, 460
Porcupine, 485
Pore canals, 220
Pores, abdominal, 322, 310
dorsal, 158
of sponges, 81
spermathecal, 157
Porifera, 81, 85
Porocytes, 81
Porpoise, 487
Portal, anterior intestinal, 662, 663, 671
posterior intestinal, 663, 665, 671
Portal systems, 329
hepatic, 329, 372, 450, 613
hypophyseal, 675
renal, 329, 372, 410
Portuguese man-of-war, 109
Postorbital process, 425
Postpatagium, 391
Postzygapophyses, 420
Potency, 686
Pouch, abdominal, of mammals, 495, 496
genital, of cockroach, 223
Prawn, 214, 234
Preaxial, 434
Preening, 390
Pre-erythrocytic cycle, 69
Prehallux, 357
Prementum, **222**
Premunition, 149
Prepubic process, 403
Prepuce, 455

Prepupa, 246
Presumptive areas, 639
Prezygapophyses, 419
Primary body cavity, 188
Primary remiges, 391
Primates, 475, *478*, 585, 618, **725**
Primitive groove, 671
knot, 663
streak, 661, 671, 674
Prismatic layer, 266
Proboscidea, 491
Proboscis of insects, *242*
Procerodes litoralis, 129
Proctodæum, 405, 654. *See also* Hind-gut
Progesterone, 676
Proglottis, 125, **126, 127**
Prolacerta, 586
Prolactin, 676
Prolegs, 254
Pronation, 434
Pronephros, 626
Pronotum, 221
Pronuclei, 632
Propatagium, 391
Prophase, 696, 700
Propodite, **196**
Proprioceptive, 619
Propterygium, 320
Prosencephalon, 616
Prosoma, 235
Prosopyles, 82
Prostate gland of leech, 182
of rabbit, 454
Prostomium of earthworm, **155,** 156, 157
of *Nereis*, 176
Protandry, 6
Proteins, 499
composition of, 7
digestion of, 441
formation of, by plant, 18
of the food, 7, 10, 442
synthesis of, 503
Proteoses, 441
Proterospongia, **39**
Prothorax, 221
Protocercal, 558
Protochordates, 309
Protogyny, 6
Protonephridium, 118
Protoplasm, 12, *498*
Protopodite, **196**,. 197
Protopterus, 552, 599
Prototheria, 496
Protozoa, 24, 76
parasitic in man, 61
Protura, 247
Proventriculus of cockroach, 225
of crayfish, 203
of pigeon, 404, 596
Proximal, 187
Psalterium, **493,** 596
Pseudobranch, 322
Pseudo-hearts, 164
Pseudonavicella, 43n
Pseudopodia, 508, 636
of *Amœba*, 24, 26
of *Hydra*, 93, 94, 97
Pseudorumination, 442
Pseudopodiospores, 43
Pseudotracheæ, 242
Psocoptera, 249
Pteraspida, 523, 557
Pterobranchia, 308
Pterodactyl, **563,** 585
Pterygota, 247
Pterylæ, 392
Ptilinum, 259
Ptyalin, 440
Pubis, 567
of frog, 356
of pigeon, 403
of rabbit, 432
Pulex irritans, 145, 259
Pulmonary cavity, 266
Pulmonata, 284
Pulp of tooth, 436
Pulse, 543
Pupa, 246
Pupil, 464
Pygostyle, 395
Pyloric sphincter of dogfish, 322
of rabbit, 438
Pylorus of frog, 363
of rabbit, 438, 469
Pyramids, 461
Pyriform lobe, 459
Pyruvic acid, 535, 536

Quill, 392
Quinine, 73

Rabbit, *414*, 484, 563
alimentary system of, 435
arteries of, **448, 450**
backbone of, 419
blood of, 450
blood vessels of, **440,** 445
brain of, 458
circulatory system of, 446
cœlom of, 417
colours of, 707
development of, 668
digestion in, 440
ductless glands of, 469

Rabbit, excretory organs of, 453
  external features of, 414
  heart of, 445
  limbs of, 414, 431
  nervous system of, 457
  reproductive organs of, 454
  respiratory organs of, 444
  sense organs of, 436, *463*
  skeleton of, 418
  skull of, **428, 430**
  thorax of, **417**
  veins of, **449, 450, 614**
  vertebrae of, **420**
Rachis, of feather, 392
  of gonad of *Ascaris*, 135
Radialia, 318, 560
Radial symmetry, 102, 107, 295
Radiolaria, 79
Radius, 286. *See also* Bone
Radula, **267,** 285
Rain worm, 141
Rami communicantes of spinal nerves, 339, 382, 385, 462, 622
Rana esculenta, 555
Rana temporaria, 344. *See* Frog
Rat, 472, 485
Ratitæ, 556
Rattus norvegicus, 472
Rays (fishes), 550
Rays, fin, 318, 558, 560
  gill, 318
Receptaculum ovorum, 172
  seminis, 270
Recessive, 689
Recombination of factors, 692
Rectrices, 392
Rectum, 630
  of cockroach, 225
  of dogfish, 323
  of frog, 363
  of pigeon, 405
  of rabbit, 438, 439
  of swan mussel, 276
  See also Canal, alimentary
Red cat, 175
Redia, 122
Reduction division, 700
Reed, **493**
Refection, 442
Regeneration, 638
  in crayfish, 202
  in earthworm, 175
  in *Hydra*, 98
  in Turbellaria, 129
Regulation, 16
  of circulation, 446
  of temperature, 190, 452
  osmotic, 29, 192, 209, 333
Reingestion, 442
Relapsing fever, 236
Relaxation, 11
Remiges, 391
Remora, 146
Renal. *See* Artery, Portal system, Vein
Repeated fission, 43n
Reproduction, 1, 2
  asexual, 6
  of *Amœba*, 32
  of *Ascaris*, 135
  of *Aurelia*, 109
  of *Carchesium*, 58
  of *Chlamydomonas*, 35
  of cockroach, 229
  of crayfish, 215
  of dogfish, 333
  of earthworm, 171
  of *Entamœba*, 62, 63
  of *Euglena*, 37
  of frog, 376
  of *Hydra*, 96
  of leech, 182
  of lancelet, 307
  of liver fluke, 119
  of malaria parasite, 68
  of *Monocystis*, 42
  of *Nereis*, 178
  of *Obelia*, 101
  of Olynthus, 82
  of *Opalina*, 60
  of *Paramecium*, 51
  of parasites, 152
  of pigeon, 414
  of *Polytoma*, 35
  of rabbit, 454
  of snail, 269
  of starfish, 293
  of swan mussel, 278, 281
  of tapeworms, 126, 130
  of *Trypanosoma*, 64
  of *Vorticella*, 57
  sexual, 6. *See also* Life-history
Reproductive organs. *See* Generative organs.
Reptilia, 555, 557
  blood vessels of, 609
  skull of, 584
  See also Lizard
Respiration, 2, 10, 18
  of *Amœba*, 28
  of cockroach, 227
  of crayfish, 208
  of dogfish, 322, 323
  of earthworm, 163
  of frog, 374
  of *Hydra*, 96

Respiration of liver fluke, 118
of parasites, 151
of pigeon, 405
of plants, 18
of rabbit, 444
Respiratory pigments, 190
system, 597
Restiform bodies of dogfish, 337
Retia efferentia, 631
Reticulum, **493**, 596
Retina, 464, 540
origin of, 624
Retinal image, 465
Retinula, **213**
Rhabdias bufonis, 142
Rhabdites, 128
Rhabditis, 133, *138*
Rhabdonema nigrovenosum, 142
Rhabdopleura, 308
Rhinal fissure, 459
Rhinencephalon, 459
Rhinoceros, 490
Rhizocrinus, 297
Rhizopoda, 78
Rhombencephalon, 616
Rhynchocephalia, 550
Rhynchota, 251
Riboflavin, 10, 536
Riboflavin-adenine-dinucleotide (FAD), 536
Ribonucleic acid (RNA), 502, 503, 504, 707
Ribosomes, 502
Ribs, 573
cervical, 421
of dogfish, 314
of pigeon, 395
of rabbit, 418, 421, *422*
vestigial, of frog, 349
Rickettsia, 251
Rima glottidis, 374
Rodentia, 483, 484
Rods and cones, 540
Rostellum, 125
Rostrum of bird, 400
of crayfish, 105
of dogfish, 316
Rough hound, 310
Round worms, 131, 138
Rumen, **493**, 596

Sacculina, 148, 150, **233**, 235
Sacculus of ear, 386, 467
rotundus, 438
Saccus vasculosus, 336
Sacral vertebræ, 350, 395, 422
Sacrum, 395, 403, 422
Sacs, air, of pigeon, 407
Sacs, lymph, of frog, 347
scrotal, 415, 454
sperm, 333, 631
vocal, of frog, 362
Saddle, 156
Sagittal crest, 425
Salamander, 555
Salamandra, 555
Saliva, 440
Salivary glands. *See* Glands, salivary
Salmo, 552
Salmon, 193
Salpingœca, **39**
Saltatorial locomotion, 484, 485, 564
Salts, inorganic, of the food, 7
Santonin, 138
Saprophytic and saprozoic organisms, 39, 138
Sarcolemma, 523
Sarcoplasm, 523
Sarcopsylla, 145
Sarcopterygii, 552
Sarcoptes scabiei, 236
Sauropsidan, 609
Sawflies, 239, *260*
Scala media, 467
tympani, 467
vestibuli, 467
Scales, cycloid, **551**
epidermal, of pigeon, 389
of reptiles, 533
of dogfish, 312
placoid, **312**
Scaphognathite, 208
Scaphopoda, 284
Scapus, 392
Schistosoma, 124
Schizogony, 69, 75
Schizont, 69, 75
Schizozoite, 69, 75
Sciurus, 485, 486
Schneiderian membrane, 468
Sclerites, 200
Sclerotic, 464, 542
Sclerotin, 220
Sclerotome, 570, 648, 665
Scolex, 124
Scorpionidea, 236
Scorpion-fly, 253
Scrotum, 415, 495, 532
Scyliorhinus, 310. *See* Dogfish
Scyllium, 310
Scyphistoma, 109, **111**
Scyphomedusæ, 109
Sea cows, 491
cucumbers, 297

Sea-gooseberries, 114
  lilies, 297
  urchins, 296, 636
Sea-anemones, *111*, 144
Seals, 489
Sebum, 532
Secondary body cavity, 189
  remiges, 391
Secretin, 469
Secretion, 11, 12, 512
  internal, 16
Sections of body, 23, 187
Segmentation, 191. *See also* Somites
  of cockroach, 221
  of crayfish, 197
  of dogfish, 312
  of earthworm, 156
  of lancelet, 299
  of leech, 179
  of ovum. *See* Cleavage
  of tapeworm, 125
  of Vertebrata, 570, 573
Segments of body. *See* Segmentation
  of limbs, **196, 223**
  of ovum. *See* Cleavage
Segregation, 692
Selenodont teeth, 492
Self-fertilisation, 121, 152
Self-preservation, 2
Sella turcica, 423
Semen, 455
Semicircular canals, 342, 386, 468
Semilunar valves of heart of dogfish, 325
  of frog, 368
  of pigeon, 407
  of rabbit, 446
Seminal vesicles, of *Ascaris*, 135
  of cockroach, 229
  of dogfish, 333
  of earthworm, 173
  of frog, 376
  of liver fluke, 119
  of man, **482**
  of pigeon, 411
Seminiferous tubules, 376, 547
Semipermeable membranes, 192
Sense organs, 540
  of cockroach, 228
  of crayfish, 212
  of dogfish, 342
  of earthworm, 171
  of frog, 385
  of lancelet, 307
  of pigeon, 412
  of rabbit, 463
  of snail, 269
  of swan mussel, 281
Sense organs. *See also* Ear, Eye, Olfactory organs, Statocyst
  -tentacle of starfish, 288
Senses of *Amœba*, 27
  of man, 480
Sepia, 285
Septa of earthworm, 158, 161
Septum, interorbital, of pigeon, 400
  nasal, 316, 423
Serpula, **184,** 185
Serum, 528
Sessile animals, 55, 297, 309
Setæ, of crayfish, 197, 214
  of earthworm and *Nereis*. *See* Chætæ
Sex, 6
  a Mendelian character, 709
  determination of, 687, 709
  linkage, 712
Sexual reproduction, 6
Shank, 415
Shards, 244
Sharks, 550
Sheep, 456, 492, **564**
  eye of, 464
  stomach of, **493**
Shell, egg. *See* Reproduction
  gland of dogfish, 333
    of liver fluke, 120
  of snail, 266
  of swan mussel, 271
Shield of crayfish, 195
Shore crab, 193
Shoulder blade, 354
Shrews, 476
Shrimp, 234
Sialis lutaria, 253
Sickle-cell anæmia, 708
Silica, 84
Silk, 235, 254
Silver-fish, 244, 247
Simplicidentata, 484
Sinu-auricular valves of frog's heart, 367
Sinus, 367
  cardinal, 603
  terminalis, 667, 671
  urinary, of dogfish, 333
  urogenital, 333, 630
  venosus, 603
    of dogfish, 324, 328
    of frog, 366
Sinuses, vascular, of chick, 666
  of cockroach, 228
  of crayfish, 205
  of dogfish, 328
  of leech, 182
  of swan mussel, 273

Siphonaptera, 259
Siphonophora, 109
Siphons of dogfish, 334
  of gnats, 256
  of swan mussel, 272
Siphunculata, 250
Sirenia, 491
Sitta, 730
Six-hooked embryo, **125,** 127
Skates, 550
Skeletal tissues, 520
Skeleton, appendicular, 418
  axial, 418
  endophragmal, 200
  mesodermal, 296
  of crayfish, 200
  of dogfish, 314
  of frog, 347
  of pigeon, 395
  of rabbit, 418
  of vertebrates, 558
Skin, as respiratory organ, 597
  of bird, **394**
  of dogfish, 311
  of frog, 344, **346,** 347
  of lancelet, 299
  of mammal, 510, 519, *531*
Skull, 578
  of *Capitosaurus*, **584**
  of cat, 431
  of cod, **581**
  of crocodile, **586**
  of dog, 423
  of dogfish, 315
  of frog, 350
  of kangaroo, **494**
  of lizard, **588**
  of man, **479**
  of *Ornithorhynchus*, 585
  of pigeon, 399
  of rabbit, **428, 430**
  of reptiles, **583,** 584
  of snake, **586**
  of *Sphenodon*, **586**
  of thylacine, **494**
  of turtle, **583**
  table of bones of, 593
Sleeping sickness, 64
Slipper animalcule, 45
Slits, gill-. *See* Gill-slits
Slow-worm, 556, 562
Snail, 264
  kidney of, 268
  nervous system, 268
  nutrition of, 267
  reproductive system of, 269
  shell of, 266
  torsion of, 266
Snakes, 556, 589, 595
Social insects, 249, 260
Soil, action of earthworms on, 156
Solar plexus, 463
Solenocytes, 118, **119,** 305, **306**
Soles of feet, 415
Somatopleure, 648, 652, 661, 671
Somites, 191, 570, **571,** 645, 648, 662, 665. *See also* Segmentation, metameric
Sorex minutus, 476
Soricidæ, 476
Spasmoneme, 56
Spatangus, 297
Special creation, 718
Specialisation, 14
Species, 22, 715
Specific name, 22, 716
Sperm, 5. *See also* Spermatozoon
  rosettes, 173
  sacs, 333, 631
Spermatheca, 173, 229, 269
Spermathecal pores of earthworm, 157, 173, 175
Spermatic cord, 454
Spermatids, 702
Spermatocytes, 97, 702
Spermatogenesis of earthworm, **174**
  of rat, **547**
Spermatophore of snail, 270
Spermatozoon, 5, 632, 702
  of *Ascaris*, 135
  of crayfish, 216
  of earthworm, **174**
  of *Hydra*, 97
  of man, **5**
  of Nematoda, 142
Sperm-mother-cells of earthworm, 173
Sphenodon, 556, 585, **586,** 609
Sphincter, pyloric, of dogfish, 322
  of rabbit, 438
Sphincters, 534
Spicules, 81
Spiders, 145, *235*
Spinal cord, 538
    of frog, 380
    of man, 538
    of rabbit, 457
  nerves, 306, 337, 382, 462
Spindles, cell-, 696
Spindle-tree, 252
Spine. *See* Vertebræ
  hæmal, of dogfish, 314
  neural, 419
  of scapula of rabbit, **432**
Spines of starfish, 288
Spinnerets, 235

Spinules of liver fluke, 115
Spiracle, 227, 310, 322, 323, 598
Spiral valve of conus arteriosus, 368
 of intestine, 323
Spireme, 706
Spirochætes, 236, 251
Splanchnocœle, 648
Splanchnopleure, 648, 652, 661, 671
Splanchnotome, 648
Spleen, 531
 of dogfish, 323
 of frog, 366
 of pigeon, 405
 of rabbit, 438
Sponge, bath, structure of, **84**
Sponge bodies, complex, 82
 simple, 81
Sponges, 81
 branched calcareous, 82
 canal systems of, **83**, **84**
 food of, 82
 larvæ of, 85
 siliceous and horny, 84
Spongilla, 85
Spore formation in *Amœba*, 32
 in *Monocystis*, 43
Spores, 43n
Sporocyst, 122
Sporont, 43, 73, 75
Sporozoa, *79*, 105, 154
Sporozoites of *Monocystis*, 43
 of *Plasmodium*, 73, 75
Springtails, 244, *247*
Squalus, 310
Squamata, 556, 585
Squirrels, 485, 565
 flying, 485
Stable-fly, 255
Stadium, 244
'Staggers', 130
Stapes, 426, 594
Starch, 8, 441
 granules in *Polytoma*, 34
Starfish, 286, 296
 alimentary canal of, 289
 behaviour of, 294
 body-wall of, 288
 cœlom of, 288
 excretion of, 290
 external features of, 286
 fertilisation of, **635**
 food of, 289
 larva of, **294**
 nervous system of, 288
 perihæmal and pseudohæmal systems of, 292
 reproduction of 293,
 water vascular system of, 291
Statocysts of crayfish, 213
 of medusa, 103
 of molluscs, 269, 281
Stearic acid, 9
Stearin, 9
Stegocephalia, **553**, 554, **567**, 573, 584, **591**
Stenohaline animals, 193, 291
Stenopodium, 197
Sternebræ, 422
Sternum of cockroach, 221, 223
 of crayfish, 194
 of frog, 355
 of lizard, **567**
 of *Ornithorhynchus*, **497**
 of pigeon, 402
 of rabbit, 418, *422*
Stick-insects, 249
Stigma (eyespot, pigment spot) of flagellates, 37
Stigmata of cockroach, 227
Stimulus, 6
 effects of, on *Amœba*, 28
 on *Hydra*, 91
 on nerve, 620
 on nerve net, 91
 on *Paramecium*, 49
Stipes, **222**
Stoat, 489
Stomach of crayfish, 203
 of dogfish, 322
 of frog, 363
 of leech, 181
 of medusæ, 102
 of pigeon, 404
 of rabbit, 438
 of ruminants, 596
 of sheep, **493**
 of snail, 267
 of starfish, 289
 of swan mussel, 275
 of vertebrates, 596
 See also Canal, alimentary
Stomodæum, 654. *See also* Fore-gut
Stomoxys, 255
Stone canal, 289, 291
Stone-fly, 245, *248*
Stratum corneum, 510
 granulosum, 510
 lucidum, 510
 of Malpighi, 510
Strepsiptera, 260
Streptostyly, 589
Strobila, 125
Strobilisation, 110
Sturgeon, **551**, 552, 559
Styella, **681**
Style, crystalline, 276

Styles of cockroach, 223
Subclass, 22
Subgenital pits, 109
Subgerminal cavity, 659
Submentum, **222,** 239
Subspecies, 717
Subumbrella, 101
Suckers of leech, 179
  of liver fluke, 115
  of tadpole, 656
  of tapeworm, 124
  of tube feet, 288
Suctoria, 80
Sugar, 8
  cane, 8
  grape, 8. *See* Glucose
  malt, 8, 441
  milk, 441
Sulci, cerebral, 458
Superfamily, 22
Superlinguæ, **222**
Supination, 434
Supradorsals, 315
Suprarenal gland. *See* Gland, adrenal
Sus scrofa, 492
Sutton, W. S., 705
Sutures, 423, 545
Swan mussel, 270. *See* Mussel, swan
Swimbladder. *See* Bladder, air
Swimming. *See* Locomotion
Sycon, 82, 84
Sylvian fissure, 458
Symbiosis, 94, *144*
Symmetrodonts, 594
Symmetry, bilateral, *187*, 296
  radial, 107, 187, 296
Sympathetic system, 527, *622*
  of dogfish, 339
  of frog, 385
  of rabbit, 462, 471
Sympathin, 622
Symphysis, 545
Symplasts, 33
Synapse, 512, 514, 621
Synapsida, 497, 589
Synapticulæ, 302
Syncytium, 33, *499*, 523, 526
  in *Ascaris*, 132
  in embryo of crayfish, 680
  in epidermis of crayfish, 197
Syndactyly, 496
Syngamy, *4*, 33, 35, 52
Synovia, 418
Synovial capsule, 418, 545
Synsacrum, 403
Syrinx, 407
Syrphids, 144, *259*
Systole, 29

Tabanids, 142, *259*
Tachyglossus, 496
Tadpole, 553, 627, 657
Tænia, 124, 151
  cœnurus, 130
  echinococcus, 130
  saginata, 126, 130
  serrata, 130
  solium, *124*, 129
  life-history of, **125,** 127
Tæniarhynchus, 126
Tail, 299, 558
  of Cetacea, 486
  of dogfish, 311, 314
  of fishes, 558
  of lancelet, 299
  of pigeon, 392, 395
  of rabbit, 414
  of tadpole, 657
  vestigial vertebræ of. *See* Coccyx, Pygostyle, Urostyle
Tail-fan of crayfish, 194
Talpa europæa, 476
Tapeworms, *124*, 129, 151
Tapirs, 490
Tarsometatarsus, 403
Tarsus of cockroach, **223**
  of vertebrates, 357, 403, 562
Taste-buds, 469
Taxis, 259
Teats, 415
Tectrices, 391
Teeth, bunodont, 480, 492
  canine, 431, 437
  carnassial, 437
  cheek, 431, 437
  diphyodont, 437
  eye, 431
  heterodont, 431
  incisor, 431, 437
  lophodont, 484, 495
  milk, 437
  molar, 437
  of dog, 431, 437
  of dogfish, 322
  of frog, 360
  of horse, **491**
  of man, upper, **483**
  of rabbit, 437
  of whales, 486
  permanent, 437
  premolar, 437
  selenodont, 492
  thecodont, 431
Tegmen, 222
Telencephalon, 616
Teleostei, 533, 552, 657
Telodendria, 514

Telophase, 700, 702
Telson, 194, 197
Temperature regulation, 190, 452
Temporal lobe, 458
Tendons, 419, *519*, 520
Tentacles of cephalopods, 285
of *Hydra*, 86, 88
of lancelet, 301
of medusa, 101
of *Obelia* polyp, 100
of sea-anemone, 111
prostomial, of *Nereis*, 176
sense of starfish,, 288
velar, 301
Tergum of cockroach, 221, 223
of crayfish, 194
Termites, 145, 244, *249*
Testacea, 79
Testes, function of hormone of, 471, 687
of *Ascaris*, 135
of cockroach, 229
of crayfish, 215
of dogfish, 333
of earthworm, 173
of frog, 376
of *Hydra*, **96,** 97
of leech, 182
of liver fluke, 119
of lizard, **631**
of mammal, 547
of pigeon, 411
of rabbit, 454
of tapeworm, **126, 127**
Tetrapoda, 553
Texas fever, 236
Thalamencephalon, 616, 674
of dogfish, 336
of frog, 383
of pigeon, 412
of rabbit, 460
Thalami, 384, 460
Thecla, 255
Therapsida, 584, 594, 609
Thiamine, 10
Thigh, 415
Thoracic duct, **451,** 530
vertebræ, 421
Thorax of cockroach, 221
of crayfish, 195
of rabbit, 417, 444
Thrips, 253
Thrombocytes, 530
Thumb, 415
Thylacinus, 495
Thymol, 138
Thymus of dogfish, 343
of frog, 365
Thymus of rabbit, 418, 445
Thyroid gland, 513
effect of secretion of, 347, 365, 469, 657
of dogfish, 325, 336
of frog, 365
of rabbit, 469
Thyroxine, 470, 686
Thysanoptera, 253
Thysanura, 247
Tibiotarsus, 403
Ticks, 236
Tipulidæ, 259
Tissue, *14*, 506
adipose or fatty, 518
amœboid, 508
areolar, 517
connective, 517
epithelial, 508
fibrous, 519
lymphoid, 531
mechanical, 508, 515
muscular, 508, 523
nervous, 514
reticular, 521, 531
skeletal, 520
Tissue culture, 506
Toad, 555, crawling, **360**
Toes, 415
Tongue, 595
of frog, 357
of pigeon, 403
of rabbit, 436, 469
Tonsil of rabbit, 436
Torsion, in snails, 266
Tortoises, 556, 584
Trabeculæ of skull, 577, 579
Trachea, 511, 519
of pigeon, 405
of rabbit, 444
Tracheæ, of cockroach, 227
Tracheoles of cockroach, 227
Transamination, 535
Transverse processes of vertebræ, 420. *See* Vertebræ
septum, 655
Tree-shrews, 478
Trematoda, 115, *129*, 150
Trench fever, 251
Treponema, 251
Tricarboxylic acid cycle, 502, 536
Trichinella, 142, 147 152, 153
Trichocephalus, 142
Trichocysts, 47
Trichomonas, **77,** 78
Trichoptera, 253
Trichuris, 143
Tricladida, 129

Tricuspid valve, 446
Trilobita, 235
Trimethylamine oxide, 333
Triploblastica, 107, *186*, 645
Triton, 555, 609, **685**
Triturus, 554
Tritylodon, 722
Trivial name, 22, 716
Trochlea, 356, **433**
Trochophore, **178**, 284, 679
Trochosphere, **178**, 183
Trogium, 250
Troglodytes troglodytes, 723
Trophoblast, 668
Trophozoite, 42, 69, 75
Trout, 552
Truncus arteriosus, 369
Trunk of frog, 345
Trypanosoma, *64*, 78
  brucei, 67, 149
  cruzi, **66**, 67
  equinum, 67
  equiperdum, 154
  evansi, 154
  gambiense, 65, 66
  rhodesiense, 67
Trypsin, 443
Trypsinogen, 443
Tryptophan, 8
Tsetse flies, 66, 255
Tuatara. *See Sphenodon*
Tube feet, 288, 291
Tuberculum, or tubercle, 422
Tubularia, 109
Tubules, of kidney, 376, 453, 545
  seminiferous, 376, *547*
Tunicata, 309, 681
Tunicin, 309
Tupaiidæ, 478
Turbellaria, *128*
Turtles, 556, **583**, 589
Tylenchus tritici, 138
Tympanic cavity, 387, 426
  membrane, 387
Tympanum, 466, 626
Typhlosole of earthworm, 161
  of swan mussel, 276
Typhus, 251

Ulcers, 63, 142
Umbilical stalk, 672
Umbilicus, 672
  of feather, 392
Umbo, 271
Umbrella, 101
Undulating membrane,
  of *Trichomonas*, **77**
  of *Trypanosoma*, 64
Undulating membrane of *Vorticella*, 55
Unguiculata, 475
Ungulata, 487
Unguligrade, 491, 492, 563
'Unicellular' organisms, 76
Urea, 11, 28, 163, 291, 333, 454, 535
Ureter, 512, 629
  of pigeon, 410
  of rabbit, 453
Urethra, 454, 512
Uria aalge, 731
Uric acid, 11, 227, 410
Urinary bladder. *See* Bladder
  organs. *See* Kidneys
  papilla, 333
  sinus, 333
Urine, 376, 410, 454
Urochordata, 309
Urodæum, 405
Urodela, 554, 567, 587, 599, 609
Urogenital papilla, 333
  sinus, 333
  system of vertebrates. *See* Kidneys
Uromastix, **568, 588**
Urostyle, 380
Ursidæ, 488
Ursus arctos, 489
Use, effects of, 687
Uterus, human, **482**
  masculinus, 454, 631
  of *Ascaris*, 136
  of liver fluke, 120
  of mammals, 476, 482, 495
  of rabbit, 456
Utriculus of ear, 386, 468

Vacuities of skull, 584
Vacuole, contractile, 193
    of *Amœba*, 29
    of *Euglena*, 37
    of *Paramecium*, 48
    of *Phacus*, **37**
    of *Polytoma*, 34
    of *Vorticella*, 57
  food, of *Amœba*, 27
    of *Paramecium*, 48
    of *Vorticella*, 57
Vagina of *Ascaris*, 136
  of leech, 183
  of marsupials, 495
  of rabbit, 456
  of snail, 269
Valves, heart, of crayfish, 204
  mitral, 446
  of dogfish, 325
  of frog, 368

Valves, heart, of pigeon, 407
of rabbit, 446
of veins, 544, **602**
semilunar, 325, 368, 407, 446
shell, of swan mussel, 270
spiral, of gut, 323, 596
of conus arteriosus, 368
tricuspid, 446
watch-pocket, 325, 368
Vane of feather, 392
Variation, 728
Vas deferens of *Ascaris*, 135
of man, **482**
Vasa deferentia of cockroach, 229
of crayfish, **215**
of dogfish, 333
of earthworm, 173
of liver fluke, 119
of mammal, 547
of pigeon, 411
of rabbit, 454
of vertebrates, 629, 631
See also Wolffian duct
Vasa efferentia of dogfish, 333
of earthworm, 173
of frog, 376
of mammal, 547
of vertebrates, 631
Vascular system, 543, *602*
of chick embryo, 666
of cockroach, 227
of cod, **604,** 608
of crayfish, 204
of dogfish, 324
of earthworm, 163
of frog, 366, 655
of lizard, **613**
of pigeon, 407
of rabbit, 445
of snail, 268
of starfish, 291
of swan mussel, 279
of tadpole, **612,** 655
See also Arteries, Veins
Vegetative pole, 634n
Vein, abdominal, 613, 615
allantoic, **667,** 672
anterior abdominal, *see* ventral abdominal
azygos, 447, 615
brachial, 372, 408
cardinal, 613, 615, 666
caudal, 329, 409
caval, 613
coccygeo-mesenteric, 409
common iliac, 482
dorsolumbar, 372
epigastric, 410
Vein, external iliac, 450, 482
external jugular, 372, 447, 615
femoral, 372, 409
genital, 450
hepatic, 305, 372, 410, 450, 613, 668
portal, 329, 372, 450, 613, 668
hypogastric, 409, 450
iliac, 409
iliolumbar, 450
innominate, of frog, 372
of man, 482
internal iliac, 410, 450, 482
jugular, 372, 447, 615
jugular, 408
lateral, 615
lingual, 372
mandibular, 372
musculocutaneous, 372
ovarian, 372
pectoral, 408
pelvic, 372
portal, 329, 450
postcaval (or inferior vena cava), 371, 408, 450
precaval (or superior vena cava), 371, 408, 447, 482
pulmonary, 371, 407, 609, 613, 615
renal, 329, 372, 409, 410, 450
portal, 329, 372, 410
sciatic, 372, 410
spermatic, 372
subclavian, 372, 447
subintestinal, 305, 602
subscapular, 372
ventral abdominal, 372, 615
vertebral, 603
vesical, 372
vitelline, 602, 613, 667
Veins, 328, 445, 544, 613
of amphibian, **614**
of dogfish, **330, 614**
of embryo chick, **667**
of frog, **371**
of pigeon, 408
of rabbit, **449, 450, 614**
structure of, 544
See also Sinuses
Velum of lancelet, 301
of medusa, 102
Vena cava of swan mussel, 270
of Vertebrata. *See* Vein, postcaval, precaval
Venous system. *See* Veins
Vent. *See* Anus
Ventral surface, 187
Ventricle of heart. *See* Heart

Ventricles of brain, 336, 383, 412, 460, 616
Ventrilateral processes, 314
Venules, 445
Vermiform appendix, 438, **482**
Vermifuges, 138
Vermis, 460
Vertebræ, 192, 418, 570
heterocœlous, 395
of dogfish, 314
of frog, 348
of pigeon, 395
of rabbit, 419
Vertebral foramen, 419
Vertebrarterial canal, 421
Vertebrata, 309, *548*
origin of, 556
Vesicle, cerebral of lancelet, 306
Vesiculæ seminales, of *Ascaris*, 135
of cockroach, 229
of dogfish, 333
of earthworm, 173
of frog, 376
of liver fluke, 119
of pigeon, 411
Vestibule of auditory labyrinth, 386
of lancelet, 301
of *Nyctotherus*, 59
of *Paramecium*, 45
of rabbit, 456
of *Vorticella*, 55
Vestigial organs, 724
Vexillum of feather, 392
Vibrissæ, 415
Vicia, 253
Villi of intestine, 438, 442, 597
Vinegar worm, 138
Vipera berus, 556
Viruses, 2, 252
Viscera, 417
Visceral arches, 316, 426
clefts, *See* Gill slits, Spiracle
hump, 264, 275
nerves of cockroach, 228
of crayfish, 212
of Vertebrata, 618
See also Sympathetic nervous system
skeleton of dogfish, 316, **317**
of rabbit, 426
of vertebrates, 587
Vision, 540. *See also* Eyes
Visual purple, 542
Vitamins, 9, 442, 471, 533, 542
curve showing effect of on growth, **9**
Vitelline membrane, 634
of bird, 659
Vitelline membrane of frog, 649
of lancelet, 640
vessels, 602, 613, 667
Vitreous humour, 464
Viviparous animals, 141, 142, 252, 335, 456
Vocal cords, 374, 444
sacs, 362
Voles, 485
Von Baer's law, 724
Von Mohl, H., 498
Vorticella, 55
Vulpes vulpes, 488
Vulva, 415, 456

Walking. *See* Locomotion
Wallace, A. R., 718
Walruses, 489
Warble-fly, 145, *259*
Warm-blooded animals, 452
Wasps, 260
Waste products of body, 11
Watch-pocket valves, 325, 368
Water as food, 7
elimination of, 210
in protoplasm, 499
Water-boatman, 251
Water-scorpion, 251
Waxy layer, 220
Weasel, 489
Webs of frog's foot, 346, **372**
Whale, blue, 487
the killer, **487**
Whalebone, 486
Whales, 486, 519, 560, 565
Wheel organ, 301
Whelks, 284
White ants, 249
White matter, 384, 457, 539, 616
White of egg, 411, 659
Wild boar, 492
Windpipe. *See* Trachea
Wings, of bat, 477
of bat and bird compared, **727**
of cockroach, 222, 223
of insects, 243
of pigeon, **389**, 390, 395, 402
Wolf, 488
Wolffian duct, 331, 376, 411, *629*
Woodlice, 234
Wren, 723
Wrist, 415. *See* Carpus
Wuchereria bancrofti, 142

Xenopsylla cheopis, 260, 485
Xiphisternum, 355, 423
Xiphoid cartilage, 355, 423
process, 402

Yellow cells, 161, 163
Yolk, 97, 499, 632
  cells, 653
  duct, 119
  glands, 120
  plug, 653
  sac, 663, 670

Zein, 8
Zona radiata, 668
Zonule of Zin, 624
Zoochlorella, 93
Zooids, 58
Zoology, 1, 21
Zoomastigina, 78
Zoothamnium, 59
Zooxanthellæ, 112
Zoraptera, 249
Zygapophyses, 419
Zygoma, 29, *192*
Zygomatic arch, 426, 427
  process, of maxilla, 427
    of squamosal, 426
Zygote, 4
  of malaria parasite, 75

MORRISON AND GIBB, LTD., LONDON AND EDINBURGH